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119. Saltman, Paul and Howard Boroughs. 1960. The accumulation of zinc by fish liver slices. Arch. Biochem. and Biophy. 86:169-174.

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Reprinted from ARCHIVES OF BIOCHEMISTRY AND BIOPHYSICS, Volume 86, No. 2, February, 1960
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ARCHIVES OF BIOCHEMISTRY AND BIOPHYSICS **86**, 169–174 (1960)

The Accumulation of Zinc by Fish Liver Slices[1]

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Received March 28, 1959

The accumulation of zinc by Puffer fish liver slices has been studied under various physical and chemical conditions.

Zinc can be accumulated by Puffer fish liver cells against an apparent sevenfold concentration gradient by a passive mechanism not directly coupled to metabolic energy.

Kinetic studies of the system reveal that this process consists of a first-order sorption of the zinc to binding sites on or within the cell. Although the binding site is not specifically characterized, it is profoundly altered by changes in temperature, pH, and chemical environment.

INTRODUCTION

The essential role of zinc for the growth and development of all living systems has long been recognized. Several excellent reviews concerning its metabolic role are available (1, 2). Major research interest has been concerned with the activities of zinc with respect to its activity as a cofactor for some metalloenzyme systems (3), its binding to insulin (4), the distribution of Zn^{65} following injection in the rat (5), and zinc deficiencies in crops (6).

Following the testing of atomic devices in the South Pacific, many marine organisms, especially fish, were found to contain high levels of Zn^{65} in various tissues (7). Marine organisms in general contain zinc in amounts which are somewhat higher than those found in other animal forms. Recent investigations of Miura and Tsunajima (8) demonstrate that Zn^{65} can be readily accumulated from the external ionic environment by goldfish. Townsley and Boroughs (unpublished) have shown that Zn^{65} fed to the fish *Tilapia mossambica* appears in all tissues within 24 hr. The fact that the zinc is carried largely by the plasma, rather than by the red blood cells as occurs in mammals, may account for the higher concentrations of zinc in fish as compared with most mammals. The elegant studies of Chipman, Rice, and Price (9) have clearly demonstrated the remarkable ability of many organisms to accumulate zinc at concentrations several thousand times greater than the sea water in which they are suspended.

The relatively large amounts of zinc accumulated by fish liver led to the use of this tissue in our studies. The effects of various chemical and physical environments on zinc uptake by isolated fish liver slices are presented in this paper, and a possible mechanism for zinc accumulation is proposed.

METHODS

Several preliminary studies were undertaken to determine the most convenient type of readily available fish liver to be used in these experiments. Most livers examined and tested were difficult to slice and disintegrated upon incubation. The liver of the Puffer fish (*Tetraodon hispidus*) was ideal both from the standpoint of availability and consistency. Puffer fish, varying in length from 8 to 14 in., were trapped and kept in flowing salt water tanks until use. At this time, the fish were sacrificed by cutting the spinal cord with scissors inserted through the gill openings. The livers were removed and chilled in ice-cold Ringer solution (see below), and cut with a Stadie-Riggs hand microtome into slices approximately 350 μ thick. The slices were blotted with filter paper, and 30–80-mg. (wet weight) aliquots were placed in 20-ml. beakers containing the reaction mixture under study.

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[1] Contribution No. 119, Hawaii Marine Laboratory. The work was supported in part by contracts between the U. S. Atomic Energy Commission and the University of Hawaii AT-04-3 (56), and the University of Southern California, AT (11-1)-113.

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It is difficult to be certain that the preparation of the slices did not destroy the integrity of all the cells and not just those of the cut surface. Microscopic observations of fixed and stained slices of fish liver before and after incubation revealed little or no destruction. Measurement of the resting potential of single cells with microelectrodes from intact and sliced mammalian livers (13) revealed no significant difference of their electrical properties. The instruments for such measurements unfortunately were not available in Hawaii to test the fish liver silces.

A special Ringer solution was prepared to contain the approximate concentrations of ions found in fish serum (10). The composition in mg./100 ml. was as follows: Na^+, 300; K^+, 20; Ca^{++}, 15; Mg^{++}, 5; Cl^-, 523. The solution was adjusted to pH 7.0 prior to use.

Zinc was supplied as $ZnSO_4 . H_2O$ and was adjusted to the desired concentration with Ringer solution. Radioactive Zn^{65} was obtained from Oak Ridge National Laboratories as $ZnCl_2$ in 0.4 *N* HCl. An aliquot of the isotope was neutralized and added to the medium to give a final concentration of approximately 3 μc. Zn^{65}/ml.

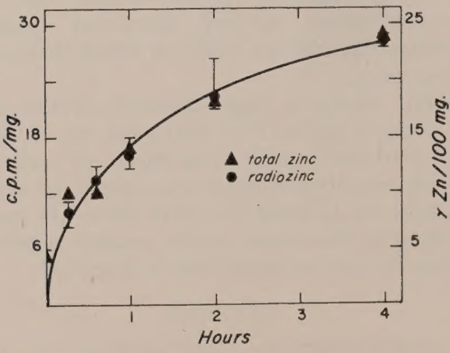

FIG. 1. The accumulation of zinc by fish liver slices as a function of time. Slices were incubated in 3.0 ml. of Ringer solution containing 30 μg./ml. zinc including 1.4 μc./ml. Zn^{65}. At intervals slices were washed and their radioactivity was measured. The slices were then wet-ashed in H_2SO_4-HNO_3, and total Zn^{++} was measured by the dithizone method.

The total volume of the reaction mixture was 3.0 ml. of Ringer solution, pH 7.0, in which was dissolved the $ZnSO_4$, the Zn^{65}, and any other compound under study. The slices were incubated for the desired interval of time with shaking at 25°, unless otherwise indicated. At the end of the incubation, the slices were washed three times with chilled Ringer solution and placed directly in 15 × 45 mm. vials for determination of radioactivity. The activity was measured in a scintillation well counter with the pulse height analyzer set at the 1.1-Mev peak. All activities were corrected to 1 mg. of wet weight. Each experimental condition was carried out in triplicate; data are expressed as the average of three values. In the experiments where total zinc determinations were made, the slices, after counting, were wet ashed by refluxing with 1.0 ml. H_2SO_4-HNO_3 (1:1 of concentrated acid). The digests were diluted with water, and suitable aliquots were analyzed for zinc by the dithizone method (11). Values for total zinc were corrected to 100 mg. wet weight.

In the experiments where efflux was studied, the tissues were incubated with Zn^{65} for 30 or 120 min., washed with Ringer solution, and then placed in a vial containing 2.0 ml. of Ringer solution with 32 μg./ml. of nonradioactive Zn^{++}. The vial containing the tissue and Ringer solution was immediately counted, then placed on a shaker at 25°. After suitable time intervals, the Ringer solution was decanted, the slices were washed three times with Ringer solution, and another 2.0 ml. of the zinc-containing Ringer solution was added. The slice and solution were counted again, and the procedure was repeated as long as desired. By such a technique the efflux of Zn^{65} from each slice can be studied over a long period of time.

RESULTS

UPTAKE OF ZINC AS A FUNCTION OF TIME

Puffer fish liver slices were incubated for various time intervals in Ringer solution containing 30 μg./ml. of Zn^{++} including 1.4 μg./ml. Zn^{65}. At the time intervals indicated in Fig. 1, the tissues were removed and washed, and the radioactivity was determined. The slices were then digested, and the total zinc was measured. As shown in Fig. 1, there is a very close parallel in the rate of uptake of both total and radioactive zinc. At the end of 4 hr. the system is saturated and no further accumulation of zinc takes place. It is important to note that the zinc is accumulated to an internal concentration approximately seven times that of the external medium.

EFFECT OF METABOLIC INHIBITORS

It was of interest to determine whether metabolic energy is required for zinc accumulation. Three inhibitors known to block various systems involving the formation of respiratory energy were tested. Slices were incubated for 30 min. at 25° in Ringer solution containing the inhibitor being studied, together with 10 μg./ml. zinc, including 5.4×10^3 counts/min./ml. Zn^{65}. The results are presented in Table I. Although there is some inhibition of zinc accumulation by dinitrophenol, it is important to realize that any "active transport" system would be completely inhibited at this concentration. Cyanide and iodoacetate considerably enhanced the rate of accumulation.

THE KINETICS OF UPTAKE AND THE ENERGY OF ACTIVATION

The time course of zinc uptake was similar to that observed for iron and copper accumulation (12, 13). A rate equation was formulated based on the postulation that zinc is accumulated by a sorption process in which the rate of accumulation is proportional to the number and the availability of specific binding sites. The total number of sites must be proportional to the amount of zinc bound at saturation, Q_s, and the number of sites occupied at any time, t, i.e., Q. The rate equation for the over-all reaction is

$$\frac{dQ}{dt} = k(Q_s - Q) \qquad (1)$$

where k is the rate constant. Integration of Eq. (1) yields

$$\ln \frac{Q_s - Q}{Q_s - Q_0} = -kt \qquad (2)$$

where Q_0 = the amount of zinc initially present.

Liver slices were incubated at 0° and 25° for various times in the Ringer solution containing 10 μg./ml. zinc including 4.5×10^3 counts/min./ml. Zn^{65}. The time course of uptake is shown in Fig. 2. It should be noted that at the higher temperature there is an increase in the initial rate of uptake as well as an increase in the amount of zinc accumulated at saturation.

TABLE I

EFFECT OF METABOLIC INHIBITORS ON ZINC UPTAKE

Liver slices were incubated for 30 min. at 25° in Ringer solution, pH 7.0, containing the inhibitor and 10 μg./ml. of the Zn^{++} including Zn^{65} (5.4×10^3 counts/min./ml.). The control contained no inhibitor. The slices were washed and radioactivity was measured.

Inhibitor	Concentration	Per cent control
	M	
Dinitrophenol	10^{-3}	74
Iodoacetic acid	10^{-3}	142
Potassium cyanide	10^{-3}	226

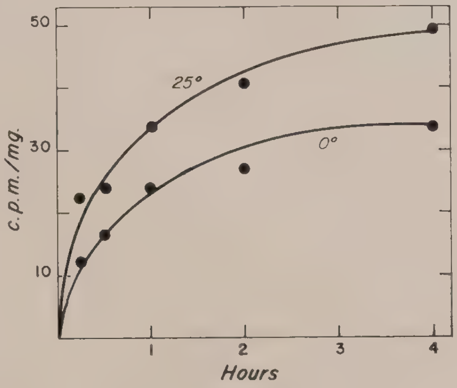

FIG. 2. The effect of temperature on zinc accumulation. Two series of liver slices were incubated at 0° and 25° in 3.0 ml. Ringer solution containing 11 μg. zinc/ml. including 4.5×10^3 counts/min./ml. Zn^{65}. At intervals slices were washed and radioactivity was determined.

If these data from Fig. 2 are plotted as log $(Q_s - Q)/(Q_s - Q_0)$ vs. t, straight lines postulated by Eq. (2), whose slopes equal $-k/2.3$ (Fig. 3), are obtained. The k values are given in the insert in Fig. 3. The energy of activation for the over-all reaction can be calculated from the Arrhenius equation and yields a value of -3.0×10^3 cal./mole/deg. The energy of activation of the initial entry of zinc into the cell calculated from the initial slopes of Fig. 2 gives a value of 4.4×10^3 cal./mole/deg. These values are certainly within the range expected for a diffusion-controlled process.

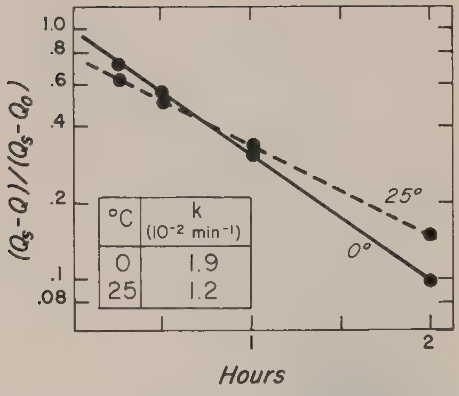

FIG. 3. Determination of rate constants for the uptake of zinc by liver slices. The data from Fig. 2 are plotted as log $(Q_s - Q)/(Q_s - Q_0)$ vs. t. The insert indicates the values for k obtained from the slices.

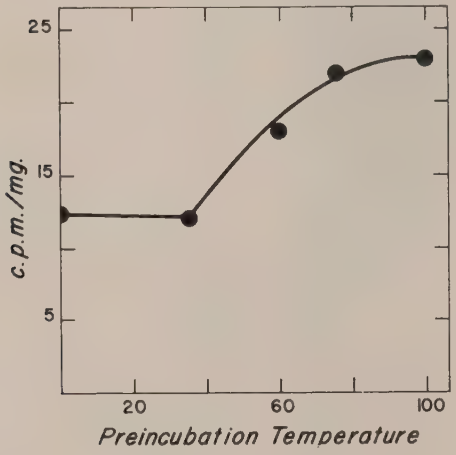

FIG. 4. The effect of pretreatment of liver slices at various temperatures on zinc accumulation. Slices were incubated for 20 min. in 3.0 ml. of zinc-free Ringer solution at the temperatures indicated. They were then transferred to 3.0 ml. Ringer solution containing 10 μg./ml. Zn, including Zn^{65}, 3.4 × 10^3 counts/min./ml. Incubation was carried out at 25° for 20 min. The slices were washed and radioactivity was determined.

PREINCUBATION AT ELEVATED TEMPERATURES

As indicated above, there is a pronounced influence of the temperature on the initial rate and amount of zinc accumulated. These changes probably reflect some sort of alteration in the zinc-binding entity which provides additional sites. Slices were preincubated for 20 min. at various temperatures in Ringer solution; they were then transferred to fresh Ringer solution containing Zn^{65} and incubated for another 20 min. at 25°. The data from such an experiment are presented in Fig. 4. An irreversible increase in the capacity of the liver cells to accumulate zinc has taken place.

THE EFFECT OF EXTERNAL ZINC CONCENTRATION

Fish liver slices were incubated for 40 min. in Ringer solution containing various concentrations of zinc from 1 to 32 μg./ml. These solutions contained activities of Zn^{65} which were directly proportional to the concentration of total zinc. Only the initial rate of uptake was measured, and not equilibrium-saturation concentrations, by selecting a 40-min. incubation period. The hyperbolic shape of the curve obtained is seen in Fig. 5*a*. These data analyzed by plotting $(Zn^{++})/v$ vs. (Zn^{++}), Fig. 5*b*, give a dissociation constant for the zinc complex of 1.4×10^{-5} *M*. Results such as these can readily be interpreted on the basis of a limited number of specific sites to which zinc is bound.

EFFLUX OF ACCUMULATED ZINC

Liver slices which had accumulated Zn^{65} for 30 or 120 min. were able to exchange the isotope with nonradioactive zinc as shown in Fig. 6. It is interesting that about 7% of the radioactivity is bound so that it cannot leave the cell. These results are similar to our observations on the efflux of iron (14) and of copper (13) from a mammalian liver, where a far greater fraction of the accumulated ion could not be remobilized once it was accumulated.

DISCUSSION

A great deal of interest has been centered on the mechanisms involved in the establishment and maintenance of concentration gradients of cations, anions, and other metabolites by various cells and tissues. Two primary mechanisms have been invoked: (*a*) active transport of substances directly dependent upon metabolic energy constantly

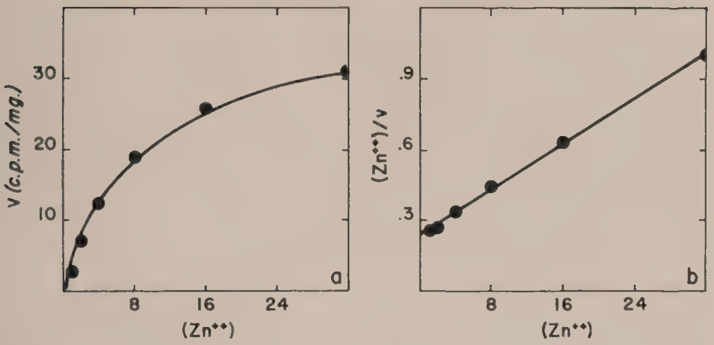

FIG. 5*a*. Effect of external concentration of zinc (μg./ml.) on its initial rate of accumulation *v*. Slices were incubated for 20 min. at 25° in 3.0 ml. Ringer solution containing the various concentrations of zinc indicated. The radioactivity in the buffer was directly proportional to the zinc concentration, specific activity, 34 counts/min./μg. Zn. The slices were washed and radioactivity was measured.

FIG. 5*b*. Analysis of the data from Fig. 5*a* by plotting $(Zn^{++})/v$ vs. (Zn^{++}).

being supplied by the cell and (*b*) passive transport of substances in response to electrochemical and thermodynamic gradients. Evidence is accumulating that some transport mechanisms consist of both an active as well as a passive component. There is a passive movement of ions into "apparent free space" prior to incorporation into plant tissues (15), in the inward movement of Na^+ in frog skin (16), in succinate going into yeast cells (17), and in many other systems. In none of these systems studied, however, was there a passive net uptake against apparent concentration gradients. The accumulation of zinc, as well as of copper and iron, by liver cells, is completely independent of metabolic energy as indicated both by inhibition studies and energies of activation. It is dependent solely on the presence of ion-binding sites within the cells.

The extensive investigations of the binding of ions by isolated proteins have been elegantly reviewed by Gurd and Wilcox (4). The general principles which apply to complex formation between metal ions and proteins [see Sec. IV, p. 338 of Ref. (4)] can be extended to the biological system studied here. Alteration of the zinc-binding sites by either physical or chemical means induces profound changes in the zinc-binding behavior of both isolated proteins and the liver slice. Gurd and Goodman (18) have demonstrated the participation of imidazole groups of human serum albumin in zinc complex formation. At present, we can make no definitive statement concerning the intimate nature of the binding site in the liver slice. The possibility that nucleic acids may serve as metal-complexing agents should not be ignored (19). There is evidence that the nucleus plays an important role in the initial phases of iron accumulation (20).

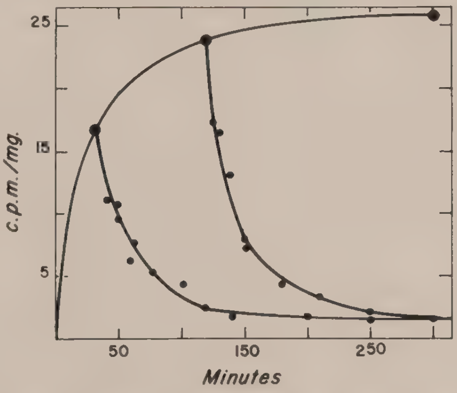

FIG. 6. Efflux of zinc from liver slices. Slices were incubated at 25° in 3.0 ml. Ringer solution containing 32 μg./ml. zinc including 2.8 μc./ml. Zn^{65}. At 30 min. and at 120 min. a series of slices was removed, washed, and placed in a glass vial with 2.0 ml. of Ringer containing 32 μg./ml. of nonradioactive zinc, and the radioactivity was measured. At the times indicated, the slices were again washed, transferred to fresh Ringer solution with 32 μg./ml. zinc, and again counted. This process was repeated until activity in the slice reached a constant value.

The effect of temperature on zinc uptake is most interesting. It is clear that both the initial rate of accumulation and the total capacity for zinc binding is enhanced at 25° as compared with 0° (Fig. 2). However, the rate constant, k, is lower at 25°. These results reflect the complex nature of the overall reaction, which involves not only the number of sites, the diffusion constant of the ion, and thermal activation, but probably many other factors as well.

It is clear that the accumulation of zinc by fish liver slices is not directly coupled to metabolic energy. Until we know the exact chemical nature of the binding sites, we are unable to explain the enhancement of the zinc accumulation with iodoacetate and cyanide. This passive mechanism involves the sorption of the ion with a rather high affinity to a site or sites on or within the cell. The zinc can be readily mobilized from such a reservoir and utilized by the organism as needed. This mechanism is compatible with the results observed by Chipman *et al.* (9) in their *in vivo* studies. A more complete study of the zinc binding proteins of various marine organisms would seem profitable.

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A New Hawaiian Percoid Fish, *Suttonia lineata,* with a Discussion of Its Relationships and a Definition of the Family Grammistidae

WILLIAM A. GOSLINE

Reprinted from PACIFIC SCIENCE
January, 1960

Reprinted from PACIFIC SCIENCE, *vol. XIV, no. 1, January, 1960*

A New Hawaiian Percoid Fish, *Suttonia lineata,* with a Discussion of Its Relationships and a Definition of the Family Grammistidae[1]

WILLIAM A. GOSLINE[2]

THE IMMEDIATE RELATIONSHIPS of the fish described here appear clear cut. However, the systematic position of the "pseudogrammid" group of genera to which it belongs is a matter of considerable controversy; the greater part of the present paper will be devoted to this subject.

The "pseudogrammid" genera (Table 1) are made up of a small number of serranid-like fishes which for the moment may be sufficiently defined as having a single enlarged (though frequently concealed) spine at the upper end of the preopercular border (Fig. 2*a*), and an incomplete or interrupted lateral line. Four genera are included in the group; they may be distinguished as follows:

1 Preopercular spine directed downward (this character not recorded for *Rhegma gregoryi* or *Pseudogramma guineensis*) 2
  Preopercular spine directed somewhat upward. No large lateral line pores between the eyes; in the adult *Aporops bilinearis* there is a frilled collar behind the tube of the anterior nostril, and just ahead of the preopercular spine is a small patch of glandular tissue that may bear black, hairlike processes .... **Aporops**

2(1) No tentacle over the eye 3
  A single, fleshy tentacle over each eye .... **Rhegma**

3(2) Preopercular spine broad-based and triangular (Fig. 2*a*) .... **Pseudogramma**
  Preopercular spine elongate and downwardly curved (Fig. 1) .... **Suttonia**

Aporops appears to be rather distinct from the other three genera. Whether *Rhegma* and *Suttonia* should be considered as more than subgenera of *Pseudogramma* is open to question.

Genus SUTTONIA Smith, 1953

TYPE SPECIES: *Suttonia suttoni* Smith, 1953 (East Africa). The only other species attributed to the genus is the one described below.

Suttonia was differentiated by Smith (1953: 549) from *Pseudogramma* and *Aporops* as follows: "Scales all cycloid. Preopercular spine large, sabre shaped and trough like. Nasal tube longer than interorbital width. Interorbital mostly naked. Palatines subparallel. A single lateral line." Aside from the fact that in the Hawaiian specimens the palatines are not particularly subparallel, there seems to be little to add or subtract from Smith's diagnosis.

Suttonia lineata new species
Fig. 1 and Table 1

HOLOTYPE: USNM 177950, 78 mm. in standard length, collected with a commercial fish poison off the Waianae coast of Oahu, Feb. 3, 1958, by Gosline, Takata, *et al.* in 10–12 fathoms of water.

PARATYPES: UH 2460, 5 specs., 36–72 mm., with the same data as the holotype.

There are VI dorsal spines in the holotype, VII in all five paratypes. In the larger specimens

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[1] Contribution No. 120. Hawaii Marine Laboratory in cooperation with the Department of Zoology and Entomology.

[2] Department of Zoology and Entomology, University of Hawaii. Manuscript received April 29, 1958.

TABLE 1

CERTAIN COUNTS IN "PSEUDOGRAMMIDS"

SPECIES	SOURCE	DORSAL	ANAL	PECTORAL	SCALES	GILL RAKERS[1]
Aporops						
bilinearis	Schultz, 1953	VII, 23–24	III, 19–21	16–18	ca 59–71	16–18
alfreei	Smith, 1953	VI–VII, 23–24	III, 21	15	80	×
japonicus	Kamohara, 1957	VII, 21	III, 16	×	ca 60	13
Rhegma						
thaumasium	Kanazawa, 1952	VII–VIII, 20–24	III, 16–19	16–18	47–52	14–17
gregoryi	Breder, 1927	VII, 15	III, 12	×	48	×
bermudensis	Kanazawa, 1952	VII–VIII, 19	III, 16	14	40–42	15
Pseudogramma						
polyacantha	Schultz, 1953	VII–VIII, 15–18	III, 15–18	17–18	ca 50–54	17–18
guineensis	Norman, 1935	VII, 20	III, 16–17	×	48?	×
brederi	Longley and Hildebrand, 1940	VII, 21	III, 17	14	50	×
Suttonia						
suttoni	Smith, 1953	VII, 23–24	III, 19	16	60	15
lineata						
Holotype		VI, –	III, –	16	64	—
Paratypes		VII, 23–24	III, 20–22	16	58–61	16

[1] Including rudiments.

the soft dorsal and anal rays are not only covered with skin and scales, but the basal portion of the rays becomes embedded in a heavy layer of fatty tissue. As a result the counts for these fins are based on only three paratypes, one in which the fins have been dissected (given first), and the two smallest: soft dorsal rays, 23, 23, 24; soft anal rays, 20, 21, 22. In the paratype dissected for the fin counts there are 5 gill raker rudiments above, 1 at the angle, and 10 rakers and rudiments below. Other counts are given in Table 1.

There seems no reason to give a long description of *Suttonia lineata,* for most of Smith's (1953) account of *S. suttoni* applies equally well to *S. lineata.* In one paratype there are two short, muscular caeca on either side of the pyloric end of the stomach. The pore configuration of the head is that of *Pseudogramma* rather than *Aporops,* i.e., there are two slitlike pores in the interorbital. There is also an especially large pore, larger than in either *Pseudogramma* or *Aporops,* at the very base of the free preopercular border. The preopercular spine is elongate, downwardly curved, and has a deep, sharply demarcated, central gutter filled with glandular tissue. There are no externally visible spines on the operculum, and the opercle itself has almost exactly the shape of that in *Pseudogramma* (Fig. 5). The teeth are about as described in *Suttonia suttoni* and almost exactly duplicate the dentition of *Pseudogramma polyacantha.* The nasal organ is also like that of *Pseudogramma* (Fig. 2*b*). As Smith (1953) has already noted, the scales on the top of the head stop short of the interorbital and the interorbital pores in *Suttonia;* in *Pseudogramma* the squamation extends forward nearly to the front borders of the eyes and surrounds the interorbital pores.

The most obvious differences between *Suttonia suttoni* and *S. lineata* lie in coloration. A color description of the latter species made after the specimens had been a week in formaldehyde is as follows: "Body reddish gray; dorsal, anal and caudal with a narrow white border. Lower half of head (below a rather abrupt transition zone running through the lower border of eye), pectorals and pelvics reddish. Upper half of head darker, except for a prominent light red middorsal band running from the dorsal origin to the tip of snout, this band most prominent forward." When first taken, the specimens had an

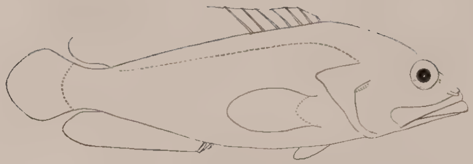

FIG. 1. *Suttonia lineata.* Paratype, 72 mm. in standard length.

essentially similar coloration. In alcohol, the smallest of the paratypes show a certain amount of reticulation on the lower portion of the head. Unlike *S. suttoni, S. lineata* has no dark opercular spot and no lines along the sides.

Aside from the characters noted in the last sentence, *S. lineata* seems to differ from the description and figure of *S. suttoni* given by Smith (1953) principally in the lack of externally visible opercular spines. The two forms are obviously close; they seem to differ to about the same degree as most Hawaiian and East African counterparts do.

Lineata (L.): lined, for the prominent mid-dorsal stripe on the head.

"PSEUDOGRAMMID" RELATIONSHIPS

Though there is little doubt about the close interrelationship of the genera assigned to the "pseudogrammid" group—*Aporops, Rhegma, Pseudogramma,* and *Suttonia*—there is considerable disagreement about the family to which these genera should be assigned (see Table 2). Regan and Norman have included them in the Serranidae; Schultz placed them in the Pseudochromidae; and Smith erected a separate family for them.

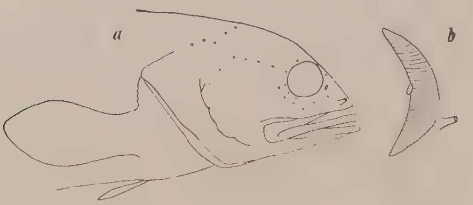

FIG. 2. *Pseudogramma polyacanthus. a,* Lateral view of head; *b,* diagram of right nasal organ, with covering tissues removed but with the position of the nostrils indicated for orientation.

In an attempt to resolve the problem of "pseudogrammid" relationships, partial or complete skeletons have been prepared of the typical serranid *Epinephelus quernus* (from Hawaii), of *Pseudogramma polyacanthus* (from Hawaii), *Plesiops corallicola* (from the Marshalls; see Inger, 1955: 266), and *Pseudochromis tapeinosoma* (from the Gilberts). Certain aspects of the soft anatomy of these species and of *Epinephelus hexagonatus* (from the Phoenix Islands), *Aporops bilinearis* (from Tahiti), *Suttonia lineata* (paratypes), and of *Grammistes sexlineatus* (from the Line Islands) have been examined. When generic names are used alone in this paper, they refer to the above species.

Soft Anatomy. The only internal soft structure that has hitherto been used in the classification of the "pseudogrammid" fishes is the presence of two heavy-walled pyloric caeca (Smith, 1953: 548, fig. 2). In *Epinephelus* pyloric caeca are relatively numerous (cf. Suyehiro, 1942: 161, fig. 112), and in *Plesiops* and *Pseudochromis* they are completely lacking.

A second feature that seems at least equally significant is the structure of the nasal rosette. In *Epinephelus, Pseudochromis,* and *Plesiops* (Fig. 3*a*) the rosette is small. In *Pseudogramma* (Fig. 2*b*) the nasal epithelium is extended both upward below the nasal bone and downward below the lacrimal.

In view of this difference between nasal organs, the brains in specimens of *Epinephelus* and *Pseudogramma* were uncovered dorsally. However, no conspicuous differences were seen.

Attempts to investigate the nature of the air bladder were unsuccessful.

In *Aporops, Pseudogramma,* and *Suttonia* there is an area of presumably glandular tissue just ahead of the preopercular spine. In *Aporops* this area may be discerned externally, but in the other two genera it is concealed by the skin and scales.

Cranium. The crania of *Epinephelus, Pseudogramma* (Fig. 4), *Plesiops,* and *Pseudochromis* differ very little from one another. In *Epinephelus* there is no conspicuous otic bulla as there is in the other three, and the supraoccipital has a well-marked crest. *Pseudogramma* has a median opening to the sensory canal system between the frontals (Fig. 4*a*), but this is lacking from the closely related *Aporops* as well as from the other three genera.

Nasal and Circumorbital Bones. In *Epinephelus, Plesiops* (Fig. 3*a*), and *Pseudochromis* the nasal bone is merely a weakly S-shaped tube bearing the front of the supraorbital lateral line. In *Pseudogramma* (Fig. 3*b*) the S-shaped tube is present but bears a flange that extends laterally over the upper end of the enlarged nasal organ.

In *Epinephelus* the first circumorbital (preorbital) is considerably expanded dorsoventrally; its upper surface articulates with the bottom edge of the lateral wing of the prefrontal, and its posterior edge is suturally joined to the small second element of the circumorbital series. It is the relatively narrow (dorsoventrally) third element that provides the subocular shelf. In *Pseudogramma* (Fig. 3*b*), *Plesiops* (Fig. 3*a*), and *Pseudochromis* the circumorbital series are similar though the preorbital covers relatively less of the surface of the head.

Jaws. The jaws and jaw teeth in *Epinephelus, Pseudogramma,* and *Plesiops* are similar. The gape is wide and the maxillary extends behind the eye; the pedicel of the premaxillary is shorter than the toothed portion; the maxillary extends well beyond the premaxillary maxillary and has a splintlike supramaxillary on its straight upper border (Figs. 3*a, b*); many of the teeth are depressible; and the teeth in the lower jaw extend well behind those of the upper and are in two or more rows throughout. In *Pseudochromis* the jaws are shorter and the teeth are all rigid; the premaxillary pedicel is at least as high as the toothed portion; the maxillary curves down around the end of the premaxillary and lacks a supramaxillary; and the teeth in the lower jaw are in a single row laterally. The teeth on the vomer, palatines, and pharyngeals of *Pseudochromis* are all rigid, as compared to the partly depressible teeth on these bones in the other three genera.

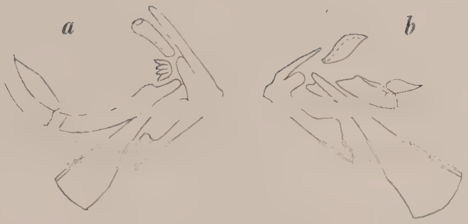

FIG. 3. First three circumorbital bones, nasals, premaxillaries, maxillaries, and supramaxillaries; teeth not shown. *a, Plesiops,* right side, with the nasal organ indicated; *b, Pseudogramma,* left side.

Suspensorium. The chief difference in the suspensoria of the four genera studied seems to be that the palatine of *Pseudochromis* is loosely articulated (apparently by ligament) to the rest of the structure, whereas in the other three it is rigidly united by suture to the ectopterygoid and mesopterygoid (Fig. 5).

TABLE 2

TAXONOMIC TREATMENT OF CERTAIN PERCOID GROUPS BY VARIOUS AUTHORS

SMITH, 1949, 1953 1954*a*. 1954*b*	WEBER and DE BEAUFORT, 1929, 1931	REGAN, 1913	NORMAN, 1957	SCHULTZ, 1953
Pseudogrammidae	to Serranidae	to Serranidae	to Serranidae	Pseudochromidae
Pseudochromidae				
Pseudochrominae				
Pseudoplesiopsinae	Pseudoplesiopidae	Pseudoplesiopidae	Plesiopidae	
Plesiopidae	Plesiopidae	Plesiopidae		
Acanthoclinidae	Acanthoclinidae		Acanthoclinidae	
Anisochromidae	—	—	—	—

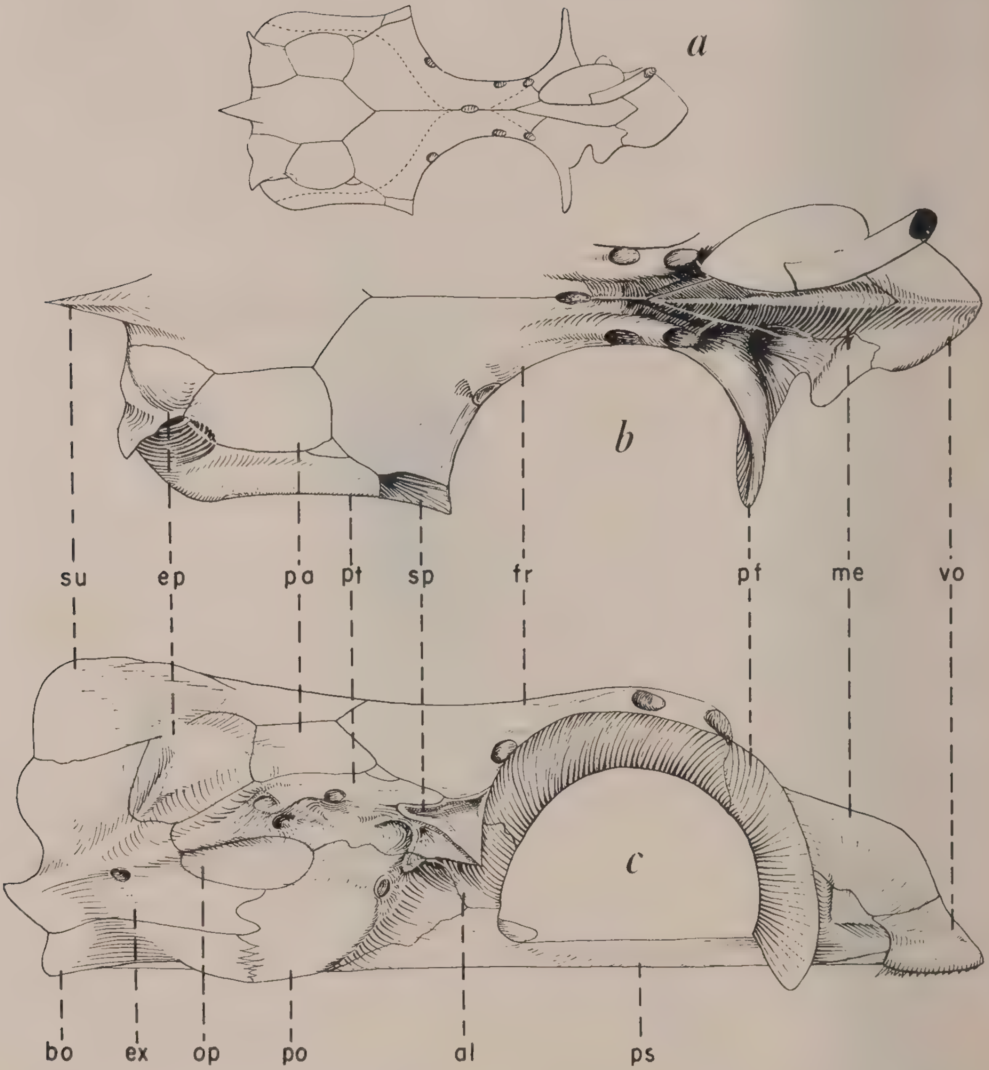

FIG. 4. *Pseudogramma. a* and *b,* Top views of the skull, with the left nasal bone in position, *a* showing the inner borders of the infraosseous portion of the supraorbital lateral line canals by dashes; *c,* side view of skull. al, Alisphenoid; bo, basioccipital; ep, epiotic; ex, exoccipital; fr, frontal; me, mesethmoid; op, opisthotic; pa, parietal; pf, prefrontal; po, prootic; ps, parasphenoid; pt, pterotic; sp, sphenotic; su, supraoccipital; vo, vomer.

Opercular Bones. The preopercle of *Epinephelus* is serrate. In *Pseudogramma* the edge is membranous except for the single enlarged spine (Fig. 5). In *Pseudochromis* the entire edge is membranous. In *Plesiops* the preopercle has a double border reminiscent of that appearing externally in some of the apogonids, but neither of these borders is serrate.

In *Epinephelus* the opercle has three superficially visible spines. In *Pseudogramma* (Fig. 5) these spines have become rudimentary and are concealed, but they can still be made out when the opercle is cleaned. The opercle of *Plesiops* ends in a frayed membrane and that of *Pseudochromis* is rounded posteriorly.

Hyoid Arch. There are seven branchiostegal rays in *Epinephelus, Pseudogramma* (Fig. 6), *Aporops,* and *Suttonia;* six in *Plesiops* and *Pseudochromis.* The branchiostegal membranes are broadly attached to the isthmus in *Pseudochromis,* attached far forward to one another but more or less free from the isthmus in the other genera. In *Plesiops* alone the third branchiostegal ray is considerably larger than those before and behind it.

Gill Arches. In all four genera skeletonized there is a pseudobranch, and the cleft behind the fourth gill arch is considerably restricted. In all, there is one pair of dentigerous lower and three pairs of toothed upper pharyngeals. In *Epinephelus* and *Pseudochromis* the gill rakers are fairly normal; the gill rakers of *Pseudogramma* and *Plesiops,* however, are in the form of flat plates at the ends of the arch with spiny knobs toward the central portion.

Pectoral Girdle. The pectoral girdle in all four genera is similar (Fig. 7) despite the fact that externally *Pseudogramma* appears to have a lobate pectoral base. In all, a long extension of the coracoid runs downward and forward to meet the cleithrum. There are two postcleithra. The forward tip of the pelvic girdles articulate with pads on the inner surfaces of the cleithra. One and a half actinosts join the coracoid and two and a half meet the scapula, though the relationship is more nearly one and three in *Pseudochromis.* The most notable difference would appear to be that there is a curious downwardly projecting hook (or, viewed conversely, an embayment) in the outer surface of the cleithrum of *Plesiops* below.

Pelvic Girdle. The pelvic girdle in all four genera consists primarily of struts between the pelvic fins and the cleithra (Fig. 7). Those of *Pseudogramma* are surprisingly strong and are longer than the pelvic fins themselves.

Vertebral Column. The number of vertebrae for several species of *Epinephelus* given by Boulenger (1895: 115) is 24. The vertebrae in *Pseudogramma* (including the terminal half-

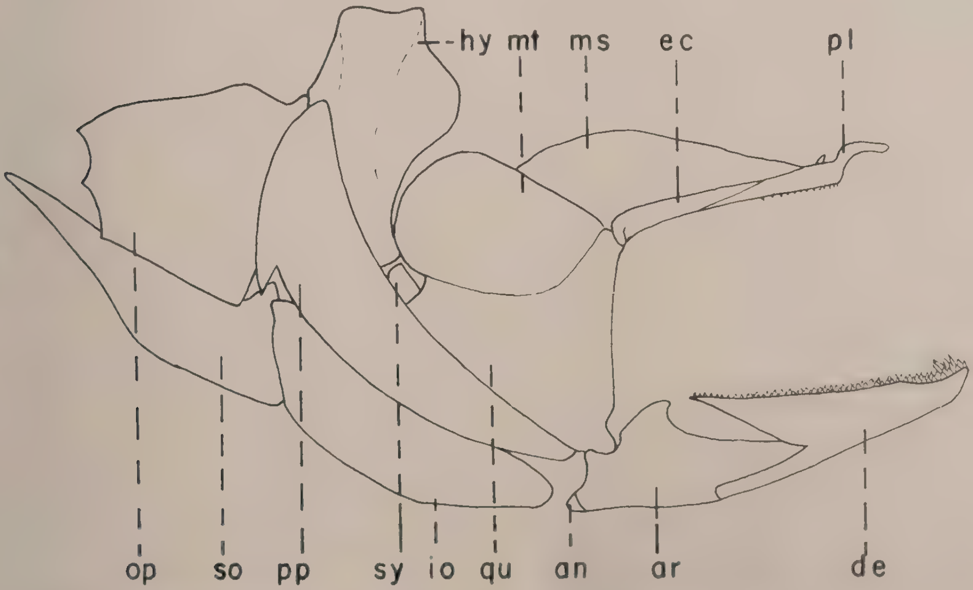

FIG. 5. Right suspensorium and lower jaw of *Pseudogramma,* external view. an, Angular; ar, articular; de, dentary; ec, ectopterygoid; hy, hyomandibular; io, interopercle; ms, mesopterygoid; mt, metapterygoid; or, opercle; pl, palatine; pp, preopercle; qu, quadrate; so, subopercle; sy, symplectic.

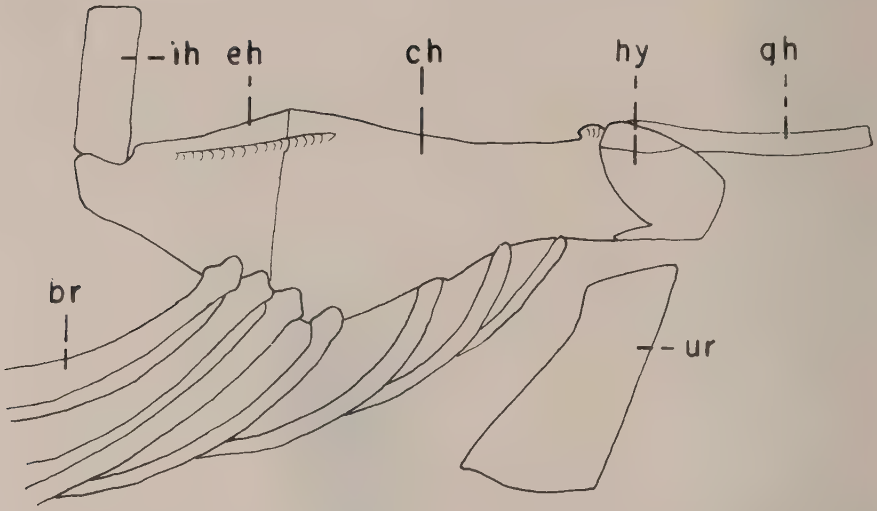

FIG. 6. Right half of hyoid apparatus of *Pseudogramma,* external view with the urohyal dislocated. br, Branchiostegal ray; ce, ceratohyal; eh, epihyal; gl, glossohyal; hy, hypohyal; ih, interhyal; ur, urohyal.

vertebra) number 26, in *Plesiops* 25, and in *Pseudochromis* 26. The first interneural in *Pseudogramma, Plesiops,* and *Pseudochromis* extends between the second and third neural arches; *Epinephelus* was not examined for this character.

In *Epinephelus* and *Pseudogramma* the second interhaemal is very strong and runs up to wedge into the posterior face of a haemal arch. In *Plesiops* and, especially, *Pseudochromis,* the second interhaemal is considerably weaker.

Caudal Skeleton. The caudal skeleton of all four genera appears to be built on the same plan (Fig. 8), though there is considerable minor variation, especially in the amount of fusion. Thus there may be two or three epurals and three to five hypurals.

Summary of Internal Differences. Though the internal, especially the osteological, differences between *Epinephelus, Pseudogramma, Plesiops,* and *Pseudochromis* are slight, they are not entirely negligible. Thus each of the three serranid offshoots stands apart in one fashion or another.

Pseudogramma differs from the other genera in the enlarged nasal organ, the preopercular spine with its associated glandular area, and in having two pyloric caecae.

Plesiops appears hardest to define on the basis of internal features. Perhaps the hook on the anterior face of the cleithrum and the double border to the preopercle are the most salient.

Pseudochromis differs immediately from the others in the mouth parts. The teeth are rigid; the maxillary bends around the premaxillary and lacks a supramaxillary; the premaxillary pedicels are elongate; and the palatines are movably articulated with the remainder of the suspensorium.

External Features. With one exception the external features of the fishes investigated will not be treated on a genus–to–genus basis as they have been noted by every ichthyologist who has worked with these groups. However, some of them will be taken up in the discussion of relationships in the next section.

The exception concerns the number of branched caudal rays. The perciform fishes are often stated to have 15 or fewer branched caudal rays. In *Epinephelus* the usual 15 were counted in 3 specimens. However, 16 are present in the one specimen available of *Grammistes.* The stained specimen of *Pseudogramma* has 17, as does that of *Pseudochromis.* In the 5 available specimens of *Plesiops,* one has 15, one 16, and three 17.

TAXONOMIC TREATMENT OF THE "PSEUDOGRAMMIDS"

The above review has indicated that there is little basic osteological difference between the serranids, "pseudogrammids," and "pseudochromids." Nevertheless there seems to be one group, traditionally included in the Serranidae, that seems to be far more closely related to the "pseudogrammids" than either *Epinephelus* or the "pseudochromids." This is the "Grammistinae" containing the genera *Rypticus, Grammistes, Pogonoperca,* and *Grammistops* Schultz, 1953 (which equals *Tulelepis* Smith, 1954). Indeed, upon analysis of the 14 characters listed in Table 3, the "pseudogrammids" fall with the "pseudochromids" rather than with the "Grammistinae" only in the lateral line and scale structure.

If the "Grammistinae" is enlarged to include the "pseudogrammids," the old distinction of this "subfamily" from the other serranids by the flap connecting the upper portion of the gill cover to the body can be retained, for this feature applies also to the "pseudogrammids." The two groups combined may be defined as follows (though it should be noted that the included genus *Pogonoperca* has not been examined):

Whole upper border of opercle attached to the body by a flap of skin. Nasal organ dorsoventrally elongate, made up of a number of

TABLE 3

COMPARISON BETWEEN "GRAMMISTINAE," "PSEUDOGRAMMIDS," AND "PSEUDOCHROMIDS"

CHARACTER	"GRAMMISTINAE"	"PSEUDOGRAMMIDS"	"PSEUDOCHROMIDS"
Operculum	joined to the skull by a membrane above	joined to the skull by a membrane above	free from the skull above
Maxillary	large, with a supramaxillary	large, with a supramaxillary	moderate to small, with or without a supramaxillary
Teeth	in bands, many depressible	in bands, many depressible	usually rigid and in one row on the lower jaw posteriorly
Nasal organ	in *Grammistes,* of numerous lamellae	of numerous lamellae	small, with few lamellae
Opercle	with 3 spines	with spines reduced, not visible externally	without spines
Preopercle	usually with 1 to 4 spines above	with 1 specialized spine above	without spines
Branchiostegal rays	6 or 7	7	6
Opercular scales	small, similar to those on body	small, similar to those on body	somewhat to greatly enlarged
Body scales	embedded, in *Grammistes* with concentric rings	about as in *Epinephelus*	about as in *Epinephelus*
Lateral line	single, complete	incomplete or interrupted	incomplete or interrupted
Dorsal and anal spines	when present, the last shorter than the penultimate	the last shorter than the penultimate	when present, the last longer than the penultimate
Dorsal and anal soft rays	basally embedded in fatty tissue in adult *Rypticus* and *Grammistes*	basally embedded in fatty tissue in adult	not embedded in fatty tissue in adult
Inner pelvic ray	attached to abdomen by a membrane	attached to abdomen by a membrane	entirely free from abdomen
Pyloric caeca	1 or 2	1 or 2	none

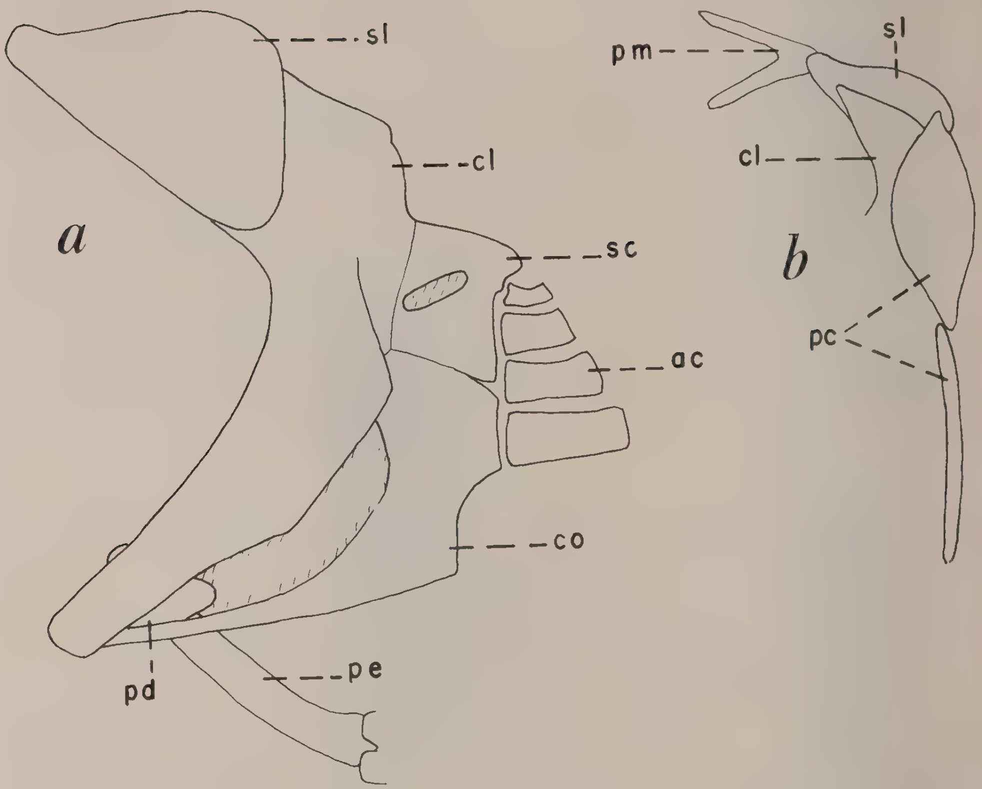

FIG. 7. *Pseudogramma. a,* Lower portion of left pectoral and pelvic girdles, from outside; *b,* upper and inner portions of right pectoral girdle, from inside and drawn to about half the scale of *a.* ac, Actinost; cl, cleithrum; co, coracoid; pc, postcleithra; pd, pad on cleithrum for articulation with pelvic girdle; pe, pelvic girdle; pm, posttemporal; sc, scapula; sl, supracleithrum.

nearly parallel, longitudinally oriented lamellae (instead of the usual rosette). Mouth large; supramaxillary present. Teeth mostly villiform, many of them depressible. No enlarged scales on operculum. Upper portion of preopercular border usually with one to four projecting spines. Two (or one) pyloric caeca. Dorsal spines II to VIII. Anal with no or with III spines, in the latter instance with the last spine shorter than the penultimate. Pelvics I, 5, the inner ray attached to the abdomen by a membrane.

The group of genera defined above seems to be sufficiently distinctive to warrant family recognition. That they are all interrelated is indicated by the rather large number of presumably independent minor characters held in common. That they deserve family rather than subfamily status is a more open question, and the author admits to considerable vacillation on this matter.

The major points in favor of family recognition would seem to be the following: (1) The genera here attributed to the Grammistidae appear to be easily and clearly distinguishable from all other percoid fishes. If intermediates exist between them and other families, they have escaped the author's notice. Apparently the closest relatives are certain members of the Serranidae, e.g., *Diploprion,* with somewhat elongate nasal organ and membranes between the pelvics and the abdomen. However, in other characters *Diploprion* falls clearly with *Epinephelus* rather than with the grammistids. (2) Although the characters differentiating the

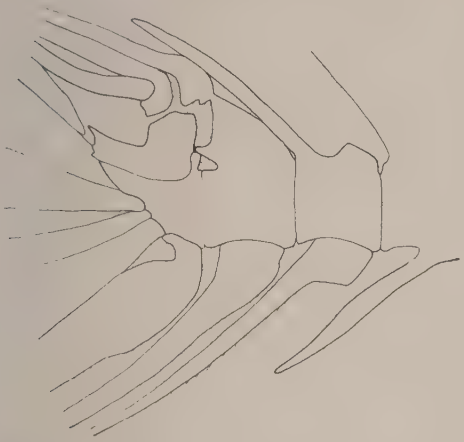

FIG. 8. Caudal skeleton of *Pseudogramma;* interosseous spaces hatched.

grammistids from related families are morphologically rather trivial, they are no more so than the features distinguishing many percoid families. In the percoids, the only alternative to such a basis of separation would appear to be the lumping of thousands of species into one or a few unwieldy families. (3) The Serranidae is already such a family. Indeed Weber and de Beaufort (1936: 555–559) have found it necessary to separate out the Serranidae at seven different points in their key to the Indo-Australian percoid fishes. Any procedure that would remove one or more of the heterogeneous elements now contained in the Serranidae would make the serranids a more manageable and more meaningful group. (4) The genera here included in the Grammistidae represent a phylogenetic lineage of respectable size. Recognition of the Grammistidae is therefore a somewhat different and, in the author's opinion, a more worthy procedure than chipping off as separate families the most aberrant endpoints of lineages. (5) From a purely practical standpoint, the retention of the grammistids, including the "pseudogrammid" genera, as a subfamily of the Serranidae would make it impossible to use the incomplete or interrupted lateral line as a basis for separating the serranids from the "pseudochromid" groups.

Nevertheless, one very valid argument can be given for retaining subfamily rank for the grammistids: that changes in status of portions of the Serranidae should not be undertaken without a consideration of the family as a whole. The author gladly admits the point. He merely feels that waiting for anything like a comprehensive review of the Serranidae is an impractical procedure.

ACKNOWLEDGMENTS

The author wishes to thank the members of the Fish Division of the Territory of Hawaii Board of Agriculture and Forestry for the facilities making possible the "deep water poison station" in which *Suttonia lineata* was collected. Comparative material in the U. S. National Museum was examined through the kind permission of Dr. L. P. Schultz; travel to that institution was defrayed by a Guggenheim Fellowship. Figures 1 and 4 were drawn by Miss Marian Adachi.

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Reprinted from THE JOURNAL OF PARASITOLOGY, April, 1960,
Vol. 46, No. 2, page 249.

A TECHNIQUE FOR MAINTENANCE OF THE SNAIL *LITTORINA PINTADO* IN THE LABORATORY.

The littorine snail, *Littorina pintado* Wood, an intermediate host of *Austrobilharzia variglandis* Penner, has a natural habitat of rocky surfaces in the intertidal zone along Hawaiian sea shores. Until recently attempts to maintain these snails in an ordinary aquarium for a long period usually ended in failure. Recently a new maintenance method has been developed and now these snails may be used for laboratory expriments with *A. variglandis.*

Medium to large snails were collected from rocky cliffs or sea benches about Oahu and Rabbit Islands. As far as possible, the schistosome-infected snails were separated from the "clean" ones in the laboratory by determining their capacity to release cercariae upon contact with sea water. These specimens constituted the experimental material for tests with this new method of maintenance.

The technique involved the use of wide-mouth gallon jars to house the amphibious snails. The jars may be inexpensively obtained after their use as food containers. Usually 20 to 40 snails were placed in each jar. Sea water was added to a depth of approximately 5 cm and the jar was covered with an inverted 8-inch finger bowl. The two pieces were then carefully turned over and more sea water was immediately added to the finger bowl to equalize the level in both containers. Thus, the snails were enclosed in a humid chamber over a reservoir of water. To keep the "aquaria" in a sanitary state, the sea water was changed twice a week.

An altrnate method which also worked effectively was the use of inverted 1-liter Erlenmeyer flasks. Each flask was fitted with a single-hole No. 9 rubber stopper into which was inserted one arm (12 cm) of a U-shaped glass tube (9mm O.D.). Ten snails were then placed in the flask after 100 ml of sea water were added. The flask was closed with the prepared stopper and inverted so that water could not enter the glass tubing. Such inverted flasks were held in place by iron ring stands or wooden racks. It appeared that provision for gaseous exchange through the tube made it necessary to change the sea water less frequently, generally only once a week, unless putrefaction of dead snails occurred.

The success of these devices relied much on the willingness of the snails to feed. The snail food employed in these expriments was a slight modification of that reported by Lee and Lewert (1956, J. Inf. Dis. **99**: 15–20). Fifty percent more water was mixed with the ingredients listed by them. The food was kept frozen in squeeze-type plastic bottles. A thin coating of this food preparation was applied to the bottom of a gallon jar or liter flask and permitted to air dry for 24 hours before the snails and sea water were added. The nutrient thus furnished lasted about 2 weeks.

By means of these methods, the "clean" snails were maintained for as long as 9 months, with a mortality rate of less than 20 percent. Snails naturally infected with schistosomes and releasing cercariae from time to time did not live for more than 1 to 2 months. Experiments are now in progress to study the survival of snails infected with schistosome miracidia in the laboratory and kept in the inverted containers at room temperature (25–30°C).

This work was supported in part by research grant No. E-2424, of the National Institutes of Health, U. S. Public Health Service. This is contribution No. 121 from Hawaii Marine Laboratory, University of Hawaii.—GEORGE W. T. C. CHU AND EDWARD PARSONS RYAN, *Departments of Bacteriology and Zoology, University of Hawaii, Honolulu, Hawaii.*

Reprinted from the Proceedings of the Malacological Society of London,
Volume 33, part 6, February, 1960

GENERIC REVISION OF THE CYPRAEINAE *

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(*Read* 12 *June* 1959)

Introduction

The genus *Cypraea* of Linnaeus, encompassing approximately 150 species, has been the subject of detailed and controversial taxonomic treatment for many years. Although many malacologists are of the opinion that the species form a comparatively homogeneous group (Ranson, 1953; Burch, 1956; Verdcourt, 1956), the genus has been extensively split. Taxonomic criteria for splitting *Cypraea* have been almost entirely conchological. The author recently proposed that the anatomical features of the species do not confirm the conchological classification (Kay, 1957). The purpose of this paper is to discuss the anatomical features which may be considered as a basis for restoring generic integrity to *Cypraea*.

Classification

The genus *Cypraea*, originally described with 42 species, was split by Gray (1824) into three genera which were grouped in the family Cypraeidae erected at that time. Subsequently Troschel (1863) split the Linnaean genus into three different genera, and Jousseaume (1884), objecting to both Gray's and Troschel's treatment of the group, described 36 genera. The family and related groups were reorganized by Thiele (1931), who established the " Stirps " or superfamily Cypraeacea. In this arrangement the Cypraeidae consists of six subfamilies of which the Cypraeinae approximates the Linnaean genus. While maintaining the term " Stirps ", Schilder and Schilder (1938–1939) elevated the Cypraeinae of Thiele to the rank of family, including in it another subfamily of Thiele, the Cypraeovulinae. The Schilders divide the Cypraeidae into four subfamilies, eight tribes, and 24 genera (excluding fossil species). The scheme of the Schilders has been modified by the Australian malacologists, Iredale (1930, 1935, 1939), Steadman and Cotton (1946), and Allan (1956), who raised several of the genera to the rank of subfamilies and introduced genera which include only one species. Allan's (1956) account of the cowries enumerates 52 genera.

Because of the controversial nature of the various taxa which have been proposed, only the subfamily Cypraeinae in the sense of Thiele (1931) will be considered in this paper. All species will be referred to the genus *Cypraea*. Authors of specific names will be cited only when the species is one which has been subject to recent revision.

Material and Methods

Cypraea caputserpentis, a widely occurring tropical species, was chosen as the representative species of the genus on which comparative studies of other species were based. It was mandatory that a single species readily available in the living state be selected for detailed morphological and histological studies since previous descriptions of the species are fragmentary and based largely on preserved material. Specimens of *caput-serpentis* were collected in the Hawaiian Islands and dissected alive and after preservation. Nineteen other species have been studied alive, and an additional 33 species have been dissected in the preserved state.

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* Contribution No. 122 of the Hawaii Marine Laboratory.

Preservation was in either 70 per cent alcohol or 10 per cent formalin. Radulae were fixed by Allen's (1952) technique and stained by the oxidation-dahlia technique of Bowell (1924).

Anatomical descriptions are limited to those appropriate to a taxonomic discussion. Detailed descriptions of the functional morphology will appear in a later paper.

ANATOMICAL FEATURES OF *CYPRAEA*

MANTLE.—The borders of the mantle are reflected over the shell and cover most of the external surface of the living animal. Mantles vary only in colour and texture. Mantle colour ranges from cream to red, brown, and black. There is some evidence that mantle colour may vary within a single species. The mantle of *annulus* was described as pale greenish white veined with black by Iredale (1935), and dark green by Steadman and Cotton (1943). *C. moneta* in Hawaii has a cream mantle distinctively veined with black; Steadman and Cotton (1943) described the mantle of Fijian specimens as spotted grey and yellow. The mantle may be smooth and velvety as in *isabella*, or variously decorated with projecting papillae. In species with papillae the appendices vary in size and structure; some are simply conical, others tentacular, branched or covered with granules. In *scurra* the papillae are large (3–5 mm. in width) and leaf-like. Descriptions of the mantle based on preserved specimens may be misleading; the papillae of *carneola* which are tufted, feathery structures in the living animal are palmate when fixed.

The differences which do exist among the species examined appear to be specific rather than indicative of groups of species which might comprise different genera. Schilder (1936) has suggested that the texture of the mantle is more useful in characterizing different branches of the Cypraeacea, i.e. different families, rather than in differentiating species groups within a single family.

Mantle Cavity.—The mantle cavity is that of a mesogastropod prosobranch, accommodating the ctenidium, osphradium, hypobranchial gland, pallial genital ducts and, in the male, a large non-invaginable penis. None of the pallial structures shows any significant deviation in structure from species to species despite Schilder's (1936) suggestion that lamellar differences in both the ctenidium and the osphradium might be of generic significance. The numbers of lamellae on the curved left ctenidium and the trifid osphradium vary among the species, but, as in the case of mantle decoration, these differences appear to be of specific nature.

Radula.—The radula is of typical taenioglossan arrangement with seven teeth per radular row in the formula 2 : 1 : 1 : 1 : 2. Differences in the structure of the teeth can be summarized by the description of four patterns, here referred to as R1, R2, R3 and R4 in the accompanying figures and table.

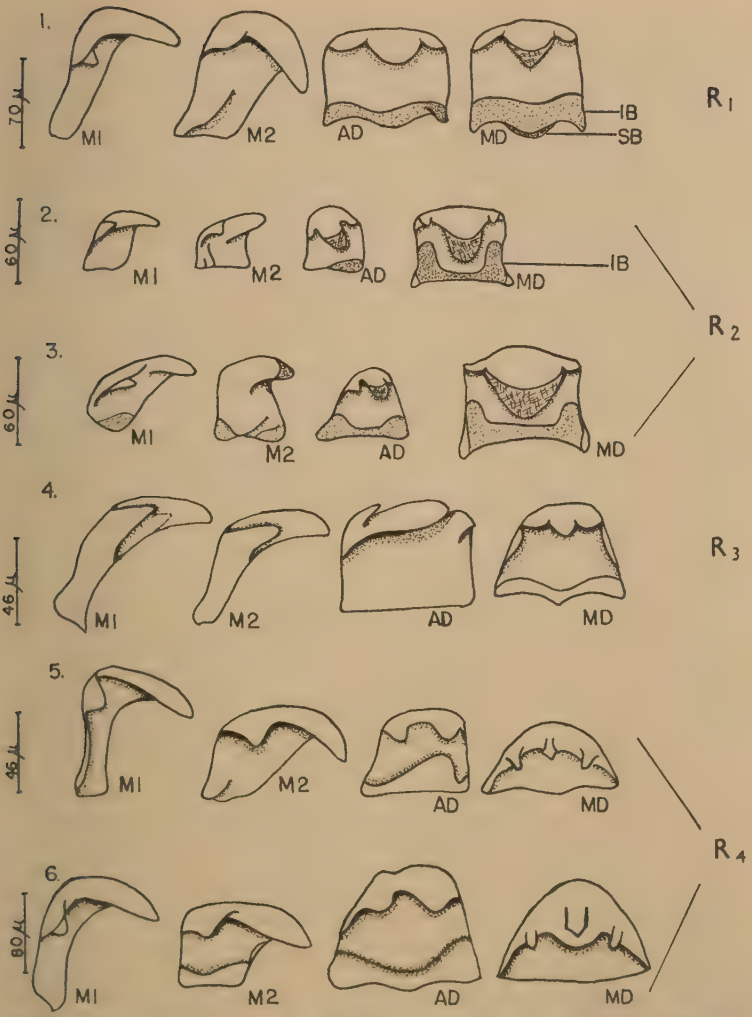

1.
70μ
M1
M2
AD
MD
IB
SB
R1
2.
60μ
M1
M2
AD
MD
IB
R2
3.
60μ
M1
M2
AD
MD
4.
46μ
M1
M2
AD
MD
R3
5.
46μ
M1
M2
AD
MD
R4
6.
80μ
M1
M2
AD
MD

Fig. 1.—*Cypraea caputserpentis*, R1. Fig. 2.—*Cypraea isabella*, R2. Fig. 3.—*Cypraea tessellata*, R2. Fig. 4.—*Cypraea teres*, R3. Fig. 5.—*Cypraea arenosa*, R4. Fig. 6.—*Cypraea sulcidentata*, R4. AD, admedian; IB, internal bract; M1, outer marginal; M2, inner marginal; MD, median; SB, subtending bract.

In pattern R1 (Fig. 1), the median and admedians are rectangular, longer than they are broad, and possess a large median cusp bordered by two smaller cusps. At the base of the median and admedians there is a dumb-bell-shaped internal bract (Fig. 1, IB) which differs in staining properties from the rest of the tooth, the bract appearing darker than the outer tooth structure. The bract extends across the basal portion of the tooth and may carry basal denticles which project toward the adjacent tooth. The denticles are lateral or medial, single or paired. Projecting below the base of the tooth there may be a semicircular element (Fig. 1, SB), which forms the border of that portion of the tooth lying against the radular ribbon. Troschel (1863) termed this the " Stutzblattchen ", which has been translated as the subtending bract. Both inner and outer marginal teeth are similar, having the form of concave blades. The long median cusp forms the blade, bordered by two shorter lateral cusps. The marginals may differ slightly from one another in the width of the tooth body. The number of radular rows varies between 50 and 125.

In pattern R2 the median tooth is pronouncedly broader than it is long, and characterized by distinctly staining internal bracts which extend vertically in the tooth (Figs. 2, 3). Basal denticles are lacking. The admedians are smaller than the median and more or less triangular in shape. The marginals are short and stout, the median cusp forming a blade-like projection. All the teeth in the radular row are distinctly separate from one another. Four species have been noted with this pattern : *isabella*, *tessellata*, *cinerea* and *talpa*.

Species of *Cypraea* which tend to be of small size, such as *kieneri*, *goodalli*, *teres* and *cribraria*, are characterized by the radular pattern referred to as R3 (Fig. 4). The median and admedians are triangular and lack both internal and basal elements. Both median and admedians remain clear and transparent when various stains are applied to them. The marginals are blade-like, overlapping each other and the admedians. The fourth pattern, R4 (Figs. 5, 6), is characterized by median and admedian teeth which are generally semicircular in shape, which lack both internal and basal elements, and which have deeply excavated cusps. The inner marginal teeth resemble the admedians ; the outer marginals are blade-like. Species which are characterized by this type of radular pattern include *tigris*, *lynx*, *vitellus*, *carneola*, *sulcidentata* and *arenosa* Gray. The number of radular rows in patterns R2, R3 and R4 usually exceeds 150.

Troschel (1863) distinguished two genera by the presence or absence of the " Stutzblattchen " in addition to conchological characters. The species examined for this study agree with Troschel's arrangement in the presence or absence of the bract except for *mauritiana*, *reticulata* Gmel., *arabica*, and *scurra*, which he included among those species lacking a subtending bract, and *cribraria* which was included with those possessing the bract. The bract is present in Hawaiian specimens of *scurra* and *mauritiana*, but absent in a specimen of *cribraria* from Guam.

Digestive System.—The digestive system displays many of the structural features of style-bearing prosobranchs, although a crystalline style is not present. The anterior esophagus extends posteriorly from the buccal bulb and curves sharply to the left, expanding immediately posterior to the nerve ring into a pouch, the mid-esophagus. The stomach is a U-shaped structure characterized by an antero-ventrally projecting caecum and a short style-sac region at the intestinal end. In living specimens, a compacted mucous rod is present in this region. A pair of diverticula extend ventrally from the anterior esophagus just posterior to the buccal bulb in a number of species. Histologically distinct areas at the same location were noted in *caputserpentis* although no diverticula are present. A single diverticulum originating in this area was described by Amaudrut (1898) in *arabica* ; this structure was not found in specimens of *arabica* from the Central Pacific.

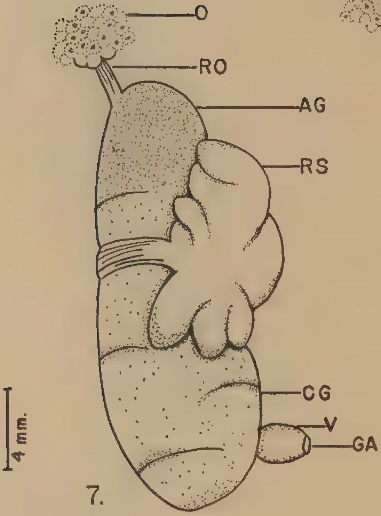
MALE REPRODUCTIVE SYSTEM.—The male reproductive system may be divided into three regions : (1) the testis which forms most of the posterior whorls of the visceral spire ; (2) the genital ducts which consist of a coiled proximal portion, the seminal vesicle and a glandular distal portion or prostate gland ; and (3) a seminal groove and penis. The latter extends from the head posterior to the right cephalic tentacle.

The only differences noted concern the size of the penis and the shape of the prostate. The shape of the penis is similar in all species, although the length and width vary from species to species. In *scurra* there is a slight constriction between the basal and anterior portions of the penis. The penial diverticulum described by Vayssière (1923) in *carneola* was absent from specimens examined from the Central Pacific and Africa. The prostate may be elongate, rectangular or club-shaped.

FEMALE REPRODUCTIVE SYSTEM.—The ovary spreads over the visceral mass anteriorly from the tip of the spire, one portion leading forward on the left side of the body parallel to the posterior esophagus, and a second, larger, portion forming the major part of the third visceral whorl. The renal oviduct (Fig. 7, RO) leaves the gonad near the kidney aperture and joins the glandular pallial oviduct which extends over the visceral mass to the right body wall. The renal oviduct opens into the albumen gland (Fig. 7, AG), an elongate, bilobed structure which joins the large capsule gland (Fig. 7, CG), distinguished by its thick lateral walls. Dorsally a short duct leads from the albumen gland to the seminal receptacle (Fig. 7, RS), a simple or diverticulated sac, which lies over the albumen gland and the posterior portion of the capsule gland. The genital aperture is at the tip of a pouch-like vagina (Fig. 7, GA).

In some species a bursa copulatrix is present, extending laterally from the vagina as a small pocket (Fig. 8, BC). In two species, *teres* and *goodalli*, the bursa lies within the vagina, and is manifest externally by a swelling of the same shape as the bursa in other species. The bursa lies within the posterior portion of the capsule gland in *kieneri* and *cribraria*. In the species with a bursa, the seminal receptacle is a glandular structure consisting of a mass of small blind tubules (Fig. 8, RS). Fretter (1941) has described a similar situation in the Stenoglossans *Ocinebra*, *Nassarius* and *Nucella* where the bursa is present and the seminal receptacle ingests effete sperm rather than accumulating virile sperm.

NERVOUS SYSTEM.—The central nervous system consists of three pairs of ganglia in the head region. The cerebral and pleural ganglia are close together in a large mass which curves over the left side of the buccal bulb and esophagus. The cerebro-pleural mass differs from that in other prosobranchs, since it is entirely lateral to the alimentary canal, and is tilted so that the right ganglia are dorsal to the left, the entire nervous mass thus twisted 90° from the theoretical morphological position. The pedal ganglia



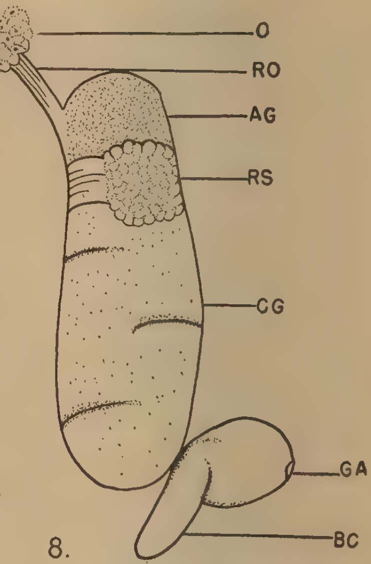


Fig. 7.—*Cypraea caputserpentis*. Lateral view of female genitalia. [*mauritiana* type, radula R1].

Fig. 8.—*Cypraea isabella*. Lateral view of female genitalia. [*tigris* type, radula R2, R3, R4]. AG, albumen gland; BC, bursa copulatrix; CG, capsule gland; GA, genital aperture; O, ovary; RO, renal oviduct; RS, seminal receptacle; V, vagina.

lie in the ventral body wall to the right of the buccal mass. The ganglia give off two long nerve cords which extend the length of the foot. On each of the pedal ganglia there is a statocyst consisting of a circular concretion lying within a ciliated epithelial sac.

Of the species examined seven require comment. In *erosa*, the whole central nerve mass is elongate, but the relationships of the ganglia are unchanged. In *tessellata* the cerebro-pleural mass is rounded in comparison with that of other species. Large pleurals (relative to the size of the cerebrals) are present in *arenosa*, *carneola*, *sulcidentata* and *cinerea*. The left pleural of *errones* Linn. is developed out of proportion to both the right pleural and the cerebrals.

Conclusions.—The species of *Cypraea* thus far examined are characterized by an extremely conservative anatomical picture. Differences in the mantle, pallial structures, male genitalia and nervous system appear to be specific rather than indicative of groups of species of generic rank. However, a distinctive combination of radular and female genitalial characters serve to distinguish two anatomical categories. In one category, henceforth referred to as the *mauritiana*-type, the radular pattern is that which has been termed R1, in which the median and admedians are rectangular with horizontal internal bracts, and the female genitalia consist of a simple vagina and saccate seminal receptacle. In the second category, henceforth referred to as the *tigris*-type, the species are characterized by the radular patterns R2, R3 and R4, either with vertical internal bracts or lacking internal bracts, without subtending bracts, and by the presence of a bursa copulatrix and glandular seminal receptacle in the female.

COMPARISON OF ANATOMICAL CATEGORIES AND CURRENT CLASSIFICATION

Comparison of the anatomical categories into which the species fall with published schemes of classification shows that the two categories cross the generic lines of Thiele's (1931) classification ; the subfamilial, tribal and generic lines of Schilder and Schilder's (1938–1939) scheme ; and the subfamilial lines proposed by Steadman and Cotton (1946).

Three of the genera described by Thiele (1931) are crossed by the two anatomical types. In the genus *Pustularia*, *nucleus*, *spurca* and *moneta* are of the *mauritiana*-type, while *tessellata* is of the *tigris*-type. In the genus *Erronea*, *hirasei* is of the *mauritiana*-type and *cribraria* of the *tigris*-type. The genus *Cypraea* is similarly divided : *mappa*, *tigris*, *lynx* and *carneola* are of the *tigris*-type, and *mauritiana* and *arabica* are of the *mauritiana*-type.

Three of the Schilders' (1938–1939) genera show similar discrepancies, and both subfamilial and tribal lines are consequently crossed by the two anatomical categories. In the Cypraeovulinae two species of the tribe Zonariini (*pyrum* and *spadicea*) are of the *mauritiana*-type, while in the Erroneini, *pallida*, *caurica*, *hirasei* and *chinensis* are of the *mauritiana*-type and *kieneri*, *goodalli* and *teres* are of the *tigris*-type. The genus *Cribraria* of the Schilders is thus split by the two categories (see Table 1). In the Cypraeinae, two species of the Cypraeorbini, *cinerea* and *isabella*, are of the *tigris*-type, while species of the Cypraeini are divided between the two anatomical categories. Within the latter tribe the genus *Mauritia* includes *mappa* and *scurra*, which are of the *tigris*-type and *arabica*, *reticulata*, *depressa* and *mauritiana* of the *mauritiana*-type. The genus *Trona* in the same tribe is likewise divided, *zebra* and *cervus* being of the *mauritiana*-type and *talpa* of the *tigris*-type.

When the scheme proposed by Steadman and Cotton (1946) is examined, discrepancies are again apparent although they are not so obvious, because of the small size of the taxa. In the Talpariinae, *talpa*, *isabella* and *cinerea* are of the *tigris*-type, and *zebra* and *cervus* are of the *mauritiana*-type. In the Erroneinae, *errones* and *caurica* are of the *mauritiana*-type and *teres* and *goodalli* are of the *tigris*-type. In the Adustinae, *pallida*, *hirasei*, *pyrum* and *spadicea* are of the *mauritiana*-type and *cribraria* is of the *tigris*-type.

Comparison of the anatomical categories with the proposed schemes of classification is summarized in Table 1.

DISCUSSION

The question raised by the preceding descriptions is whether or not anatomical features are of value in elucidating relationships among the

TABLE 1.

Species	Anatomical Categories		After Thiele (1931)	After Schilder (1938–39)	After Steadman and Cotton (1946)
	mauritiana (R1)	*tigris*			
tessellata		× (R2)	*Pustularia*	Nariinae—Pustulariini *Pustularia*	Cypraeidae *Ponda*
nucleus	×		,,	Nariinae—Nariini *Staphylaea*	Staphylaeinae *Nuclearia*
granulata	×			,,	,,
staphylaea	×		,,	,,	*Staphylaea*
spurca	×		,,	*Erosaria*	Erosariinae *Ravitrona*
helvola	×			,,	,,
caputdraconis	×			,,	,,
caputserpentis	×			,,	,,
poraria	×			,,	,,
erosa	×			,,	*Erosaria*
miliaris	×			,,	,,
lamarcki	×			,,	,,
turdus	×			,,	,,
annulus	×			*Monetaria*	*Ornamentaria*
moneta	×		,,	,,	*Monetaria*
obvelata	×			,,	*Ornamentaria*
annettae	×			Cypraeovulinae—Zonariini *Zonaria*	Adustiinae *Zonaria*
pyrum	×			,,	,,
spadicea	×		*Zoila*	,,	,,
arabicula	×			*Zonaria*	Erosariinae *Pseudozonaria*
hesitata	×		*Umbilia*	Cypraeovulinae—Umbiliini *Umbilia*	Umbiliinae *Umbilia*
pallida	×			Cypraeovulinae—Erroneini *Erronea*	Adustiinae *Gratiadusta*
hirasei	×		*Erronea*	,,	,,
onyx	×			,,	*Adusta*
pyriformis	×			,,	*Gratiadusta*
errones	×			,,	Erroneinae *Erronea*
caurica	×			,,	*Ovatipsa*
fimbriata	×			*Palmadusta*	Nariinae *Paulonaria*
quadrimaculata		× (R3)		*Blasicrura*	Erroneinae *Blascicrua*
kieneri		× (R3)		,,	Nariinae *Evenaria*
goodalli		× (R3)		*Cribraria*	Erroneinae *Talostolida*
teres		× (R3)		,,	,,
chinensis	×			,,	*Ovatipsa*
gaskoini	×			,,	Adustiinae *Cribraria*
cribraria		× (R3)		,,	,,
cinerea		× (R2)		Cypraeinae—Cypraeorbini *Luria*	Talpariinae *Luria*
isabella		× (R2)	*Talparia*	,,	*Basilitrona*
exanthema	×		*Cypraea*	*Trona*	*Macrocypraea*
cervus	×		,,	,,	,,
talpa		× (R2)	*Talparia*	,,	*Talparia*
mappa		× (genitalia only)	*Cypraea*	Cypraeinae—Cypraeini *Mauritia*	Cypraeinae *Leporicypraea*
arabica	×		,,	,,	Mauritiinae *Arabica*
scurra	×			,,	,,
reticulata	×			,, (= *maculifera*)	,, (= *arabica histrio*)
depressa	×			,,	,,
mauritiana	×		,,	,,	*Mauritia*
tigris		× (R4)	,,	*Cypraea*	Cypraeinae *Cypraea*
lynx		× (R4)	,,	,,	*Lyncina*
vitellus		× (R4)		,,	*Mystaponda*
carneola		× (R4)	,,	,,	*Ponda*
sulcidentata		× (R4)		,,	,,
arenosa		× (R4)		,,	,, (= *schilderorum*)

species of the Cypraeinae. An analysis of the relationships of four species will illustrate the significance of anatomical characters.

Ostergaard (1928) on the basis of conchological features suggested that *sulcidentata* and *tessellata*, which are both endemic to the Hawaiian Islands, were derived from the wide-ranging Pacific species *arenosa*. He pointed out that *arenosa* approaches *tessellata* in the shallow, narrow interstices between the teeth, and that *arenosa* resembles *sulcidentata* in colour pattern. Steadman and Cotton (1946) also on conchological grounds, but on the basis of shell shape and size, group all three species in their genus *Ponda*. The Schilders (1938–1939), however, place *tessellata* in the Nariinae and *sulcidentata* and *arenosa* in the Cypraeinae, distinguishing the two subfamilies by mantle characters, number of radular rows and shell characters.

Anatomical studies show such a pronounced similarity in the radular pattern and genitalia of *sulcidentata* and *arenosa* (Figs. 4, 5) that Ostergaard's hypothesis of their relationships seems confirmed. However, the radula and genitalia of *tessellata* resemble those of *isabella* (Figs. 2, 3) more closely than those of other species occurring in Hawaiian waters. As it is unlikely that one species, even though wide-ranging, would give rise to two endemic species over a comparatively short interval of time (the emergent limestones of Hawaii date from the Pleistocene), and as the range of *isabella* is such that *tessellata* could have been derived from it in Hawaii, the anatomical evidence linking *tessellata* to *isabella*, and *arenosa* to *sulcidentata* provides a more plausible explanation of the relationships than do conchological features.

The arguments against existing systems of classification of *Cypraea* are primarily concerned with the awkward taxonomy which results from splitting genera, and the consequent difficulty of discerning relationships among the species involved (Burch, 1956; Verdcourt, 1956). The fact that the anatomical categories described above cross the lines of the existing systems of classification is evidence that the systems are untenable. Unfortunately, despite the value of anatomical characters as taxonomic criteria, it is not possible at present to propose a comprehensive revision of the species. Only one-third of the living species have been available for anatomical study; if two or more genera were proposed on the basis of anatomical patterns, two-thirds of the species would be left without generic title. I am proposing that the use of all generic names assigned to species of the Cypraeinae in the sense of Thiele (1931), with the exception of *Cypraea*, be discontinued. Whether or not malacologists will agree to so radical a revision of the Cypraeinae as a permanent scheme, most will probably agree to the expediency of the inclusion of the species in one genus at least as a temporary measure.

SUMMARY

The species of *Cypraea* which have thus far been examined, exhibit little anatomical differentiation except in the structure of the radular teeth and in the pattern of the female genitalia. Two anatomical categories have been defined on the basis of these differences, here referred to as the *mauritiana*- and *tigris*-types. These anatomical categories cross the generic,

tribal and subfamilial lines of the existing systems of classification, which is evidence that the present systems are untenable. It is proposed, therefore, that only the genus *Cypraea* be retained for species of the Cypraeinae.

ACKNOWLEDGMENT

I am greatly indebted to Lt. Col. R. J. Griffiths, at present of Melbourne, Australia, for supplying many of the preserved animals and radulae which have been utilized in this study.

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Reprinted from ENDOCRINOLOGY
Vol. 66, No. 2, February, 1960
pp. 295-303

CORTICOSTEROID PRODUCTION BY INTERRENAL TISSUE OF TELEOST FISHES[1]

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ABSTRACT

Evidence has been obtained suggesting that the interrenal gland of teleost fishes is capable of secreting adrenocortical steroids. Several species of teleosts were used, and the anterior or head kidneys, containing the interrenal tissue, were incubated *in vitro*. Tentative identification of steroid secretory products was achieved, in most cases by chromatography of extracts in toluene-75% methanol and development with triphenyltetrazolium chloride.

A single spot, having the same mobility as cortisol, was obtained from the incubated tissue of *Anoplopoma fimbria* (sablefish). Spots corresponding to cortisol and cortisone were observed after incubation of the head kidneys of *Mugil cephalus* (mullet). Cortisone was tentatively identified in extracts of the incubated tissue from *Tilapia mossambica* (cichlid), as well as a substance with a polarity similar to, but not identical with, corticosterone. A fourth species, *Bodianus bilunulatus* (a'awa), failed to yield any detectable steroid, despite the relatively large number of animals used.

ALTHOUGH the interrenal organ of teleosts is thought to represent adrenocortical tissue (1), there has been no direct evidence that this gland does in fact secrete adrenocortical hormones. In 1954 Hatey (2) and Fontaine and Hatey (3) demonstrated the presence of 17-hydroxycorticosteroids in the blood of salmon (*Salmo salar*), and since that time further information has been obtained concerning the presence of adrenal steroids in teleost blood. Cortisol has been found in the blood of several species: *Gadus morrhua* (4), *Pseudopleuronectes americanus* (5), *Cyprinus carpio* (5, 6, 7), and *Fundulus heteroclitus* (7). Hatey (6) found traces of corticosterone as well as cortisol in the blood of *Cyprinus carpio*. Both cortisol and cortisone have been demonstrated in the blood of *Oncorhynchus nerka* (8), and of *O. tschawytscha* and *Salmo gairdnerii* (9). Although changes in interrenal histology have been correlated with alterations in the level of circulating adrenal steroids (3, 9), these observations offer no direct proof that the interrenal is the source of these hormones.

Received October 6, 1959.

[1] Aided in part by research grant No. G-8805 from the National Science Foundation.

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[4] Contribution No. 123 from the Hawaii Marine Laboratory.

Recently, Phillips and Mulrow (10) showed that anterior kidney tissue of the killifish *Fundulus heteroclitus* is capable of converting progesterone to adrenal steroids (cortisol, cortisone, and aldosterone) *in vitro*. This observation is the first direct evidence that enzymes characteristic of adrenocortical tissue are present in the region of the kidney containing interrenal gland.

In the present study, we have attempted to obtain evidence that the interrenal is capable of elaborating adrenocortical steroids, and to compare the secretory patterns in several teleosts, by adaptation of the Hofmann incubation method (11) to fish tissues. Four teleost species were used: *Anoplopoma fimbria* (sablefish: marine), *Bodianus bilunulatus* (a'awa or spot wrasse: marine), *Mugil cephalus* (mullet: euryhaline littoral) and *Tilapia mossambica* (cichlid: freshwater).

MATERIALS AND METHODS

Animals

Anoplopoma fimbria, the sablefish, of the family Anoplopomidae, were collected west of San Juan Island in August of 1958 and of 1959[5] at the University of Washington's Friday Harbor Laboratories. *Tilapia mossambica*, a cichlid introduced into Hawaii, were obtained from a reservoir near Ewa, Oahu, Hawaii, through the cooperation of Mr. Kenji Ego and Mr. Richard Yoshida of the Territorial Division of Fish and Game at the end of 1958 and the beginning of 1959. Some of these freshwater fish were moved into seawater aquaria 6 weeks prior to sacrifice. *Mugil cephalus*, the mullet, of the family Mugilidae, were obtained in late 1958 and early 1959 by commercial seining from the shores of Kaneohe Bay on the windward side of Oahu, Hawaii, with the help of Mr. Lester Zukeran of the Hawaii Marine Laboratory. *Bodianus bilunulatus*, the a'awa or spot wrasse, of the family Labridae, were trapped by commercial fishermen off Oahu, Hawaii, in the spring of 1959, and were made available by the cooperation of Mr. Spencer Tinker and his staff of the Honolulu Aquarium.

Incubation

In all species except *Anoplopoma fimbria*, the osmotic pressure of the blood was determined by a modification of the melting point method of Gross (12). A concentrated stock solution of medium was made, containing the following concentrations of solutes (mM./l.): NaCl, 200.0; KCl, 5.0; $CaCl_2$, 3.0; $MgCl_2$, 2.0; $NaHCO_3$, 1.0; NaH_2PO_4, 10.0; glucose, 6.0. This solution was made approximately isosmotic to the blood by dilution with distilled water. The final concentrations were as follows: *Tilapia* from fresh water, 0.16M; *Tilapia* from sea water, 0.21M; *Mugil* (marine, littoral), 0.22M; *Bodianus* (marine), 0.22M. In one experiment with fresh-water *Tilapia*, the medium was 0.20M. No blood determinations were made on *Anoplopoma* (marine), and a 0.11M solution was used.

Tilapia, *Mugil*, and *Bodianus* all possess a pair of discrete head kidneys, which were dissected out and cut into small pieces in the incubating medium. Usually the head kidneys of two animals were placed in a single flask (10 ml. Erlenmeyer) containing 3 ml. of medium. The flasks were gassed with pure oxygen for 5 minutes, stoppered, and incubated in a Dubnoff metabolic incubator at room temperature. The medium was changed and reoxygenated at the end of ½ hour, and again after the next 1½ hours of incubation. After a final 1½ hours, the tissue and the three changes of medium were pooled and frozen. In some experiments, the medium from the first ½ hour of incubation was discarded.

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[5] We are indebted to Professor Paul Illg and Mr. Hugh Stanky for the collection of additional sablefish material.

Inasmuch as there is no distinct head kidney in *Anoplopoma*, the expanded anterior portion of the trunk kidney was removed. The tissue from each animal was placed in a separate flask (25 ml.) with 6 ml. of medium. The tissues were incubated for 2½ hours at room temperature by bubbling oxygen directly into the medium through a hypodermic needle. The medium was not changed during the incubation. Tissues and media were stored frozen prior to extraction.

Extraction

The medium and tissue from each flask was extracted three times with two volumes of ethyl acetate. The ethyl acetate extract was washed with 3 ml. of 0.05N Na_2CO_3, and then washed twice with 3 ml. of distilled water. The extracts from several incubation flasks were pooled, and the ethyl acetate distilled off under vacuum at 40–45° C. The residue was further purified by partitioning between distilled water and n-hexane (Skellysolve B). The aqueous phase was re-extracted three times with ethyl acetate. The final extract was again dried down, and stored in the deep-freeze.

Chromatography

The residue was dissolved in 50 μl. absolute methanol and spotted on Whatman #20 filter paper. Standard steroids were applied to lanes running parallel to the unknown samples. Most of the chromatograms were run for 6–8 hours at room temperature in a toluene-75% methanol system (13), after equilibration overnight. One of the pooled *Tilapia* extracts that had been stored in the deep-freeze for 2½ months was run in cyclohexane-benzene-methanol-water (100:50:100:25) (10) for 24 hours at room temperature. The *Bodianus* extract was first chromatographed in cyclohexane-benzene-methanol-water for 24 hours; following this, three areas (corresponding to the location of cortisol plus cortisone, corticosterone, and 11-dehydrocorticosterone) were eluted with methanol and separately rechromatographed in toluene-75% methanol.

In most cases, identification of steroids was achieved by comparing their relative mobilities with those of the standards run simultaneously after development with triphenyltetrazolium chloride (TPTZ) (14). The *Tilapia* strip run in cyclohexane-benzene-methanol-water was sprayed with 2N NaOH, and the fluorescent spots observed under ultraviolet light (15). The *Bodianus* chromatograms were cut lengthwise in half; one half was treated with TPTZ, the other examined by the soda-fluorescence method.

Histology

Representative paraffin sections were made of the head kidneys or anterior trunk kidneys, corresponding to the regions taken for incubation. The presence of interrenal gland was confirmed, and the nature of the surrounding tissues, also included in the incubation, was determined. Tissues were fixed in Bouin's and stained with alum-hematoxylin and eosin.

RESULTS

Anoplopoma fimbria. The anterior kidneys of 17 animals were incubated, and two chromatograms were run in the toluene-75% methanol system (Fig. 1). A single spot, with a mobility identical to that of cortisol in this system, appeared on each chromatogram after development with TPTZ.

The histologic appearance of the interrenal gland and surrounding tissues

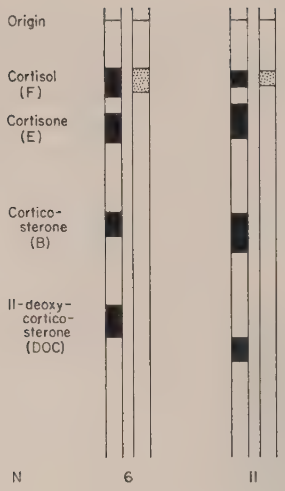


FIG. 1. Chromatographic analysis of steroids from *Anoplopoma fimbria*. Stippled spots represent the unknown substances, black areas correspond to the standard steroids run simultaneously. N indicates the number of animals used in each experiment. The incubation medium was 0.11M. Chromatograms were run in toluene-75% methanol and developed with TPTZ.

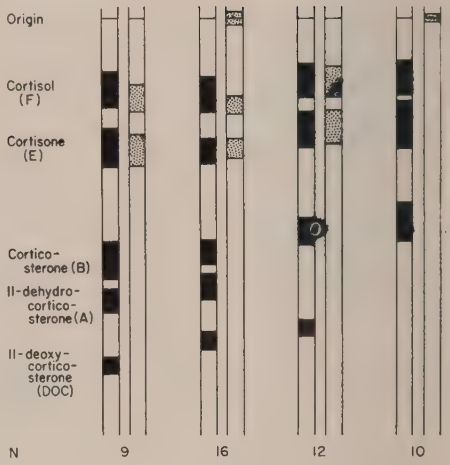


FIG. 2. Chromatographic analysis of steroids from *Mugil cephalus*. Standard and unknown steroids are shown as in Figure 1. The incubation medium was 0.22M. All chromatograms were run in toluene-75% methanol and developed with TPTZ.

is shown in Figure 4. Strands of interrenal cells are found surrounding small veins, scattered through the anterior kidney. A few chromaffin cells may be found in these areas, but most of the chromaffin tissue is embedded in the walls of larger blood vessels. Kidney tubules and hemopoietic tissue, predominantly lymphoid, make up most of the surrounding tissue of the anterior kidney.

Mugil cephalus. 47 animals were used, and 4 chromatograms were run in toluene-75% methanol (Fig. 2). On three of these, TPTZ-positive spots were found opposite the cortisol and the cortisone standards. Two of the chromatograms also had TPTZ-positive material remaining at the origin. The fourth chromatogram revealed only the spot on the starting line. The significance of this spot remains to be determined, as all our standard steroids moved off the origin in this chromatographic system.

Figure 5 shows the histology of the mullet head kidney, which is morphologically distinct in this species. Large masses of interrenal tissue surround the major branches of the postcardinal veins. Small clumps of lightly stained cells, presumably chromaffin, are found close to the blood vessel lumina. No renal elements are found in this region. The surrounding hemopoietic tissue is chiefly myeloid, but lymphoid tissue is also prominent.

Bodianus bilunulatus. Although the extracts from 34 animals were pooled and chromatographed together, no steroids were detected by either TPTZ or the soda-fluorescence methods.

The histology of the head kidney is shown in Figure 7. Although the head kidney is morphologically discrete, it is predominantly a mass of renal tubules, with lymphoid tissue visible between these. Clumps of pale chromaffin cells are widely scattered through the interrenal, which surrounds many of the larger veins and their branches.

Tilapia mossambica. 129 animals were used, and 7 chromatograms run (Fig. 3). After chromatography in cyclohexane-benzene-methanol-water and development by the soda-fluorescence method, two spots were observed. The less polar of these was found opposite the corticosterone standard, and the polar component appeared as a band from the origin through the region occupied by cortisol plus cortisone. Two of the toluene-75% methanol chromatograms, representing 8 and 14 animals, revealed no spots after treatment with TPTZ, and are not shown in Figure 3. A spot corresponding to cortisone was seen on a third, and a fourth toluene-75% methanol chromatogram showed 3 spots: one at the origin, one corresponding to cortisone, and one slightly less polar than corticosterone. All of these were TPTZ-positive.

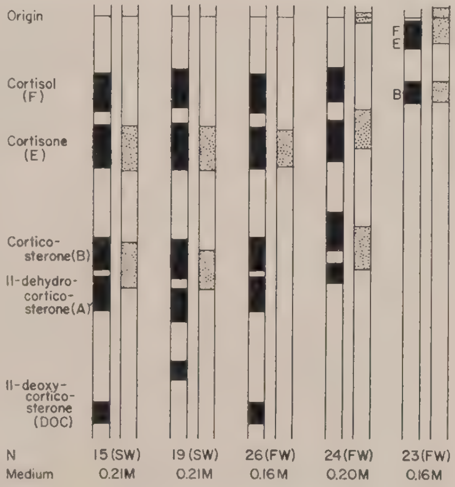
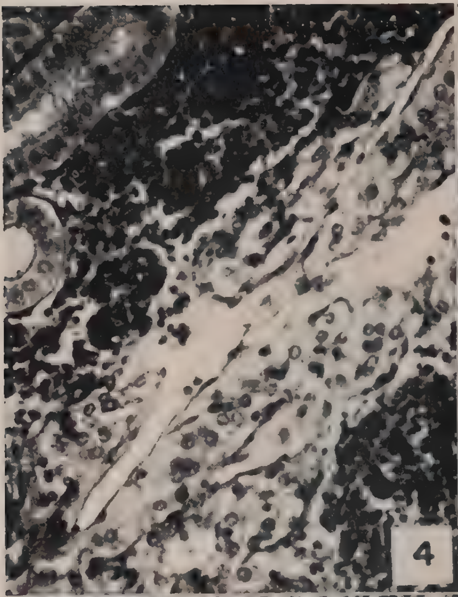


FIG. 3. Chromatographic analysis of steroids from *Tilapia mossambica*. Standard and unknown steroids are shown as in Figure 1. N indicates the number of animals used, SW refers to animals maintained in sea water for 6 weeks prior to incubation of the head kidneys, FW refers to fish taken directly from fresh water. The first four chromatograms were run in toluene-75% methanol and developed with TPTZ. The last chromatogram was run in cyclohexane-benzene-80% methanol and developed by the soda-fluorescence method.

Both experiments run with seawater-adapted *Tilapia* revealed a TPTZ-positive spot corresponding to cortisone, and one having a slightly greater mobility than corticosterone.

Figure 6 shows the histology of the interrenal and the head kidney, which is discrete in this species. The hemopoietic tissue appears to be predominantly myeloid, and no renal elements are present in the tissue associated with the interrenal. The interrenal resembles that of *Mugil cephalus*, except that no chromaffin cells have been distinguished in this area.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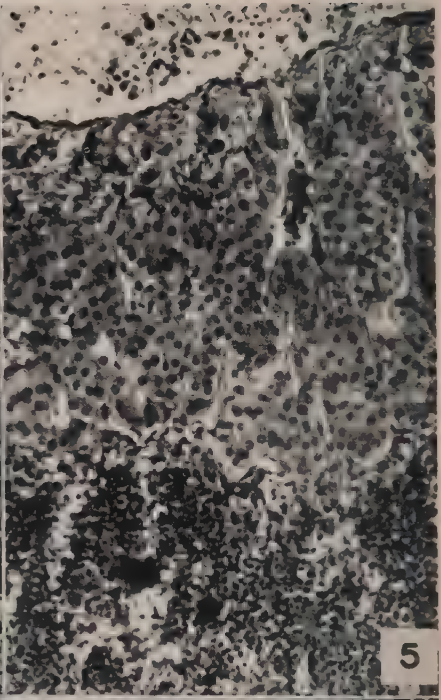
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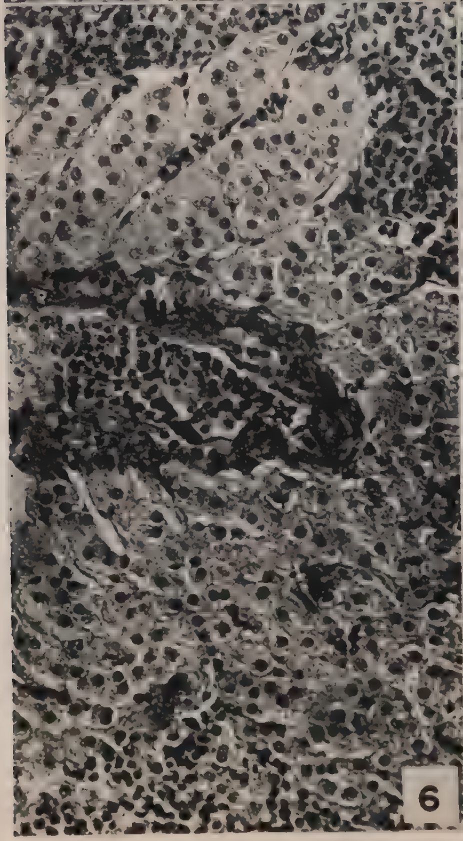
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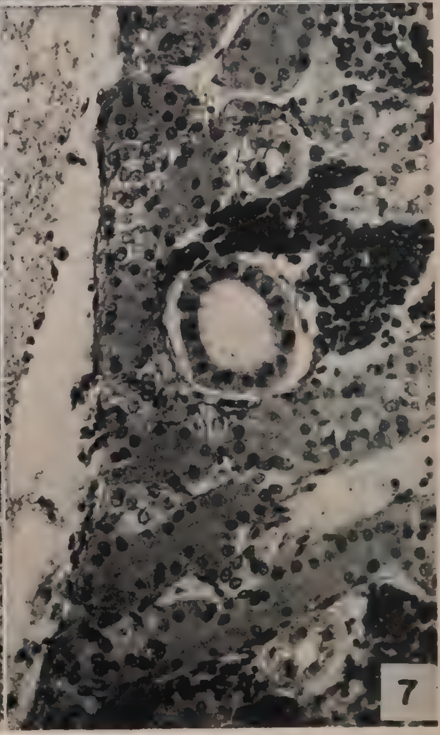
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DISCUSSION

The results (summarized in Table 1) presented herein strongly suggest that the interrenal gland of teleosts is capable of producing corticosteroids. This is further substantiated by the fact that in the rainbow trout (*Salmo gairdnerii*), relatively large quantities of control tissue (trunk kidney or liver) fail to yield detectable amounts of steroid (16). It should be emphasized, however, that the identification of the secretory products is still tentative, in most cases based only upon the mobility of the substances in a single solvent system, and upon their reaction with TPTZ. In all cases only small quantities of material, in the order of 2–5 micrograms (based on comparison with known quantities of standard), were obtained.

TABLE 1. CORTICOSTEROID SECRETORY PATTERN AND HISTOLOGIC COMPOSITION OF ANTERIOR KIDNEYS IN SEVERAL TELEOST FISHES

Species	Normal habitat	Total no.	No. of chromatograms	Steroids indicated				Presence of discrete head kidney	Histology		
				Cortisol	Cortisone	Corticosterone	11-dehydrocorticosterone		Presence of kidney tubules	Predominant hemopoietic tissue	
										Lymphoid	Myeloid
Mugil cephalus	marine	47	4	+	+	−	−	+	−	+	++
Anoplopoma fimbria	marine	17	2	+	−	−	−	−	+	+	
Bodianus bilunulatus	marine	34	1	−	−	−	−	+	+	+	
Tilapia mossambica	fresh-water	107[1]	5[1]	−	+	?		+	−		+
Salmo gairdnerii[2]	fresh-water	80	7	+	±	±	−	−	−	+	+

[1] Two additional chromatograms, using 22 more fish, revealed no spots.
[2] Nandi, J. Unpublished observations.

Despite the preliminary nature of these results, they are in general agreement with the observations of other workers on the corticosteroids present in teleost blood. The predominance of relatively polar steroids (cortisol and cortisone) is evident in all teleosts thus far examined. However, *Tilapia* represents the first teleost in which no evidence of cortisol secretion has

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FIG. 4. Histology of the anterior kidney of *Anoplopoma fimbria*, showing interrenal cells. Kidney tubules are present at the upper left. The remainder of the tissue is chiefly lymphoid. H. and E. ×370.

FIG. 5. Histology of the head kidney of *Mugil cephalus*. The lumen of a vein appears at the top. The interrenal cells extend as cords into the surrounding tissue which contains both myeloid and lymphoid elements. H. and E. ×370.

FIG. 6. Histology of the head kidney of *Tilapia mossambica*. Cords of interrenal cells surround a vein, and extend into the surrounding tissue which is predominantly myeloid. H. and E. ×370.

FIG. 7. Histology of the head kidney of *Bodianus bilunulatus*. The lumen of a vein is seen at the left. Masses of interrenal cells lie along this vein and also its branches, as seen at the lower right. The pale cells visible in this tissue are presumably chromaffin. Several kidney tubules and a collecting duct can be seen. The hemopoietic tissue is chiefly lymphoid. H. and E. ×370.

been found. Since only a few species have as yet been studied, no correlation can be made between the observed secretory pattern and the habitat, physiology, or taxonomic position of the species. That the secretory pattern of a given species does not alter with a change in habitat is suggested by the fact that the major components were the same in both freshwater and seawater-adapted *Tilapia*. There is some indication, however, that the secretory capacity of the tissue may have been somewhat greater in the seawater-adapted fish. Hane and Robertson (9) also found no qualitative variation in the blood corticoids of salmon under different environmental conditions.

A number of factors complicates the use of *in vitro* methods with teleost material. The histology of the incubated tissue reveals the presence of several tissue types other than interrenal: chromaffin tissue, hemopoietic tissue, and in some cases renal tubules are present. Work currently in progress on the rainbow trout (*Salmo gairdnerii*) indicates that the presence of these tissues may result in considerable loss of extractable steroid through some type of tissue binding. The possibility of subsequent metabolic alterations of the secreted steroids by the surrounding tissues, particularly by kidney tubules, also must be considered. These factors undoubtedly account in part for the low yield of steroids in our system. Extensive conjugation of steroids by the masses of renal tubules of the *Bodianus* head kidney, for example, may have been responsible for our failure to obtain sufficient quantities for identification in this species.

The microanatomic nature of the anterior kidney cannot be predicted by gross anatomic considerations. The discrete head kidneys of *Tilapia* and *Mugil* are free from renal elements, but the equally discrete head kidney of *Bodianus* is largely renal in structure. On the other hand, the anterior end of the trunk kidney in *Salmo* shows no renal component, whereas that of *Anoplopoma* is definitely renal. Variations in the nature of the hemopoietic "background" tissue are also considerable (see Table 1).

As in any *in vitro* system, one cannot assume that the secretory products observed correspond to those normally secreted by the interrenal gland. Preliminary experiments with the rainbow trout, using the same methods described herein, indicate the presence of cortisol, and possibly of cortisone and of small amounts of corticosterone (16). This compares favorably with the finding of cortisol and cortisone in the blood of the same species by Hane and Robertson (9).

Because of the small yield of steroid, our results probably represent only the major products of secretion from the teleost interrenal. This is equally true of the analyses of fish systemic blood. Thus, we have not yet been able to determine, for example, whether aldosterone is secreted by the teleost interrenal, although the finding by Phillips and Mulrow (10) that progesterone can be converted to aldosterone by anterior kidney tissue is highly suggestive. In addition, Phillips, Holmes and Bondy (17) have evidently detected aldosterone in the blood of male sockeye salmon. The yield of steroids from our incubations might well be increased with modifications of the incubating medium by addition of corticotropin preparations, by addition of substrates involved in steroid biosynthesis, and by alterations in ionic composition. Mammalian corticotropin preparations were not used in the present study to avoid possible pharmacologic effects, but may provide information of considerable interest (18). The addition of small amounts (approximately 0.1 Armour ACTHAR unit per 100 mg. of anterior kidney tissue) of ovine corticotropin to the incubation medium apparently increased, but did not qualitatively alter, the secretory products of the trout interrenal (16).

Further experiments are now in progress to provide more complete identification of the teleost corticoids, as well as to further define the interactions of non-interrenal tissue with steroids in our *in vitro* system.

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Reprinted from PACIFIC SCIENCE, *vol. XIV, no. 2, April, 1960*

Contributions to the Knowledge of the Alpheid Shrimp of the Pacific Ocean

Part V. The Indo-Pacific Members of the Genus *Athanas*[1]

ALBERT H. BANNER and DORA MAY BANNER[2]

THE FOUR PAPERS previously published in this series have dealt with Alpheid shrimp by geographical areas. For this paper, because a major revision of the genus is needed and the shrimps upon which the revision is based come from many different regions of the Pacific, it was considered better to deal with the genus as a whole. Some of the specimens here discussed have been reported in the four previous studies. Those specimens which have not been listed in the previous studies come from three major sources: specimens collected on the Coral Atoll Investigations made by the Pacific Science Board; specimens collected by the senior author travelling in the central Pacific under a grant from Bernice P. Bishop Museum, Honolulu; and specimens collected at Eniwetok and other Marshall Islands, by the senior author and by others under the sponsorship of the Atomic Energy Commission. In this paper, details on collections are not given; these can be found in previous or future papers.

The present study has been supported by National Science Foundation Grant NSF-G-1754. The authors wish to acknowledge their indebtedness to L. B. Holthuis for the use of the bibliography of species of higher crustacea prepared by him; without this help the list of references would have been almost impossible to prepare, especially in Honolulu where the libraries lack many of the older works.

Since the genus *Athanas* was first described by Leach in 1814, some 43 specific and subspecific names have been applied to the members of this genus, only 7 of which are not known from the Pacific and Indian oceans. The shrimp in this genus are small and inconspicuous; as a result most of the previous workers had only a few specimens, often broken, upon which to base their description; further, of the Indo-Pacific species, at least 18 have not been reported since their original capture.

The Indo-Pacific genus *Arete,* long accepted as being closely related to *Athanas,* has a somewhat similar history. Since the genus was erected by Stimpson in 1861 for the species *A. dorsalis,* 11 names have been applied to species within the genus, and 4 of these names have been based upon 3 specimens or less.

The specimens available for this study were in some cases collected in large numbers. As will be discussed below, almost all of the species which are so represented show marked variation with size and sex in the form of the large chelae, and several species appear to vary considerably in the form of the rostrum and teeth of the carapace about the eyes. As these are the chief characteristics that have been used in the separation of many of the species, a revision of the two genera is necessary. Unfortunately, the present collections do not contain representatives of enough species to permit a monographic revision, so the purpose of this paper will be to merely initiate such a revision, which other workers from other parts of the Indo-Pacific may elaborate upon and finish.

ANNOTATED BIBLIOGRAPHY OF THE SPECIES OF *Athanas* AND *Arete*

In the following listing, all species placed in these genera have been listed with reference to the original description and all subsequent Indo-Pacific records. The number of specimens upon which the original description or subsequent redescription were based has been given, wherever possible, together with the localities where the specimens were collected. Most synonyms are indicated in this listing; in the synonymies later in the paper, reference is made back to this listing.

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[1] Contribution No. 124, Hawaii Marine Laboratory. Manuscript received November 1, 1958.

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Athanas nitescens (Leach) (described as *Palaemon nitescens*), 1814. Edinb. Encyc. 7: 401. [Not Indo-Pacific.]

Athanas edwardsii Audouin, 1827. Explication sommaire des planches de Crustacés de l'Égypte et de la Syrie, ed. 2, vol. 22, pp. 249–290. Atlas Hist. Nat. vol. 2, Crustacea, pls. 1–13. [Citation taken directly from the bibliography of Holthius. For discussion of date of publication, see Sherborn, C. D., 1897. Proc. Zool. Soc. Lond., pp. 285–288.] [Now *Alpheus edwardsii.*]

Athanas monoceros (Heller) (described as *Alpheus monoceros*), 1861. S.B. Akad. Wiss. Wien 44: 274; Red Sea. [Coutière, 1899: 61, 62, makes this a variety of *A. dimorphus* Ortmann 1894, a procedure contrary to the rules of zoological nomenclature.]

Athanas mascarenicus Richters, 1880. Beitr. Meeresfauna der Insel Mauritius und der Seychellen, Decapoda, p. 164; Mauritius or Seychelles. [Coutière (1896: 381) states that Richters' specimen is too incompletely described or figured; in 1899: 33, he states this is a synonym of *Arete dorsalis* Stimpson; in 1905: 868, he stated he could not identify it with certainty with any known species.]

Athanas alpheoides Czerniawsky, 1884. Obshchestvo Īspuitateleĭ Prīroduc prī Imperatorskom Khar'kovskom Universītetye (Société des Naturalistes à l'Université Impériale de Kharkow) 13: 26. [Not Indo-Pacific. Coutière (1899: 37) states this is a juvenile.]

Athanas transitans Czerniawsky, 1884. Trans. Soc. Univ. Kharkov 13: 25. [Not Indo-Pacific.]

Athanas transitans longispina Czerniawsky, 1884. Trans. Soc. Univ. Kharkov 13: 25. [Not Indo-Pacific.]

Athanas veloculus Spence Bate, 1888. Challenger Reps. 24: 529, pl. 96, fig. 1. [Not Indo-Pacific.]

Athanas dimorphus Ortmann, 1894. Denkschr. Med.-Naturw. Ges. Jena 8: 12, taf. 1, fig. 1; 3 specimens from Dar es Salaam, East Africa.

——— Coutière, 1897b. Bull. Mus. Hist. Nat., Paris 3(7): 301. [Here Coutière placed his species *A. dispar* in synonymy.]

——— Coutière, 1903. Bull. Soc. Philom. Paris IX, 5(2): 77, fig. 12; Red Sea, New Caledonia. [Drawing of large chela of female.]

——— Balss, 1915. Ergebn. Zool. 30: 21; 1 specimen from the Red Sea.

——— Tattersall, 1921. J. Linn. Soc. (Zool.) 34: 371, pl. 28, figs. 23, 24; 1 specimen from the Red Sea. [Partial redescription.]

——— Gurney, 1924. Zool. Res. Cambridge Exp. Suez Canal, p. 260. [Larval development.]

——— Balss, 1927. Trans. Zool. Soc. Lond. 22: 222; 1 female from Dar es Salaam, East Africa. [Record of capture.]

——— Gurney, 1927. Trans. Zool. Soc. Lond. 22: 260, fig. 63. [Larval development.]

——— Kollmann, 1937. Ann. Fac. Sci. Marseille II, 10: 145, figs. 16–17. [Journal unavailable.]

Athanas nitescens veloculus Coutière, 1896. Bull. Mus. Hist. Nat., Paris 2: 380. [Not Indo-Pacific.]

Athanas leptocheles Coutière, 1896. Bull. Mus. Hist. Nat., Paris 2: 381; 1 specimen from the Red Sea. [Coutière (1897: 233) stated these were females of species renamed *A. dispar.*]

Athanas leptocheles monoceros Coutière, 1896. Bull. Mus. Hist. Nat., Paris 2: 381; 4 specimens from the Red Sea. [Coutière (1896: 381) considered *A. transitans longispina* a synonym of this species.]

Athanas solenomerus Coutière, 1896. Bull. Mus. Hist. Nat., Paris 2: 381; 1 specimen from the Red Sea. [Coutière (1897: 233) stated this was the male of the species he renamed *A. dispar.*]

Athanas dispar Coutière, 1897. Bull. Mus. Hist. Nat., Paris 3: 233; several specimens from Djibouti. [Coutière (1897: 301) stated this was a synonym of *A. dimorphus* Ortmann.]

Athanas dispar monoceros Coutière, 1897. Bull. Mus. Hist. Nat., Paris 3: 233 (in a footnote). [See *A. monoceros* above and *A. dimorphus monoceros* below.]

Athanas djiboutensis Coutière, 1897. Bull. Mus. Hist. Nat., Paris 3: 233; 2 specimens from Djibouti.

——— Coutière, 1899. Ann. Sci. Nat. VIII, 9: 62, fig. 4; p. 177, fig. 207. [Discussion of rostrum and chela.]

——— Coutière, 1903. Bull. Soc. Philom. Paris

IX, 5(2): 75; specimens from the Maldive and Laccadive Archipelagoes. [Characteristics and general distribution.]

——— Coutière, 1905. Fauna and Geog. Maldive and Laccadive Archipelagoes 2(4): 856, fig. 129. [Same as the above.]

——— Nobili, 1906. Ann. Sci. Nat. IX, 4: 31; 1 specimen from the Red Sea. [Locality only.]

——— Nobili, 1907. Mem. R. Accad. Torino IIa, 57: 353; 2 specimens from the Tuamotus Archipelago. [Brief remarks.]

——— Tattersall, 1921. J. Linn. Soc. Zool. 34: 368, pl. 28, fig. 25; 9 specimens from the Sudanese Red Sea. [Description of specimens.]

——— de Man, 1922. Siboga Exped. $39a^4$(5): 21; 1 mutilated specimen from Indonesia. [Description of specimen.]

——— Edmondson, 1925. Bull. Bishop Mus., Honolulu 27: 9; 1 specimen from Wake Island. [Record of capture.]

——— Gordon, 1935. Ann. Mag. Nat. Hist. X, 16: 629; Christmas Island, Indian Ocean. [Record of capture.]

——— Boone, 1935. Bull. Vanderbilt (Oceanog.) Mar. Mus. 6: 119, pl. 31; 2 specimens from Marquesas Islands. [Extensive description.]

——— Ramadan, 1936. Bull. Fac. Sci. Egypt. Univ. 6: 12; 4 specimens from Ghardaqa, Red Sea. [Remarks on chelae.]

——— Kollmann, 1937. Ann. Fac. Sci. Marseille II, 10: 145. [Reference not available.]

——— Gurney, 1938. Sci. Rep. Gr. Barrier Reef Exped. 6: 54, figs. 249–252. [Discussion of larval forms.]

——— Armstrong, 1941. Amer. Mus. Novit. (1137): 5; 1 female from Samoa. [Record of capture.]

——— Barnard, 1946. Ann. Mag. Nat. Hist. XI, 13: 388; specimens from Mozambique. [Locality only.]

——— Barnard, 1950. Ann. S. Afr. Mus. 38: 732–733, figs. 137 e–f; 1 specimen from Mozambique. [Brief description.]

——— Chace, 1955. Proc. U. S. Nat. Mus. 105(3349): 16; 11 specimens from the Marshall Islands. [Brief remarks.]

——— Banner, 1956. Pacif. Sci. 10(3): 322; 22 specimens from the Mariana Archipelago. [Brief discussion.]

——— Banner, 1957. Pacif. Sci. 11(2): 193; 2 specimens from the Marshall Islands. [Record of capture.]

Athanas sulcatipes Borradaile, 1898. Proc. Zool. Soc. Lond., p. 1011, pl. 65, fig. 9; 8 specimens from Funafuti. [Coutière (1905: 856) stated this was a synonym of *A. djiboutensis*.]

——— Anonymous, 1899. Mem. Aust. Mus. 3: 518; specimen from Funafuti. [Record of capture.]

Athanas ortmanni Rankin, 1898. Ann. N. Y. Acad. Sci. 12(11): 251, pl. 30, fig. 7. [Not Indo-Pacific. Now *Salmoneus ortmanni*.]

Athanas dimorphus monoceros (Heller) Coutière, 1899. Ann. Sci. Nat. VIII, Zool. 9: 61, 62. [Change of name, see *A. monoceros* Heller, 1861, above.]

Athanas naifaroensis Coutière, 1903. Bull. Soc. Philom. Paris IX, 5(2): 77, figs. 14–16; 1 specimen from the Maldive Archipelago.

——— Coutière, 1905. Fauna and Geog. Maldive and Laccadive Archipelagoes 2(4): 859, fig. 131. [Same description as the above.]

——— Coutière, 1905. C. R. Acad. Sci., Paris 140: 737. [Review of species listed in Maldive and Laccadive Report.]

——— de Man, 1922. Siboga Exped. $39a^4$(5): 16, pl. II; fig. 9; 1 specimen from Indonesia. [Description of specimen.]

——— Barnard, 1950. Ann. S. Afr. Mus. 38: 731, figs. 136 f–i; 1 specimen from Natal, South Africa. [Brief description.]

Athanas areteformis Coutière, 1903. Bull. Soc. Philom. Paris IX, 5(2): 79, figs. 17–18; 2 specimens from the Maldive Archipelago.

——— Coutière, 1905. Fauna and Geog. Maldive and Laccadive Archipelagoes 2(4): 860, fig. 132. [Same description and figures as above.]

——— Coutière, 1905. C. R. Acad. Sci., Paris 140: 737. [Review of species listed in Maldive and Laccadive Report.]

——— Balss, 1915. Ergebn. Zool. 30: 21; specimen from the Red Sea. [Locality only.]

——— Chace, 1955. Proc. U. S. Nat. Mus. 105(3349): 21; 1 specimen from the Marshall Islands. [Locality only.]

Athanas minikoensis Coutière, 1903. Bull. Soc.

Philom. Paris IX, 5(2): 76, figs. 9–11; 1 specimen from Laccadive Archipelago, Indian Ocean.

——— Coutière, 1905. Fauna and Geog. Maldive and Laccadive Archipelagoes 2(4): 858, fig. 130. [Same specimens and figures as the above.]

——— de Man, 1911. Siboga Exped. $39a^1$(2): 149, pl. 2, figs. 5–5h; 2 specimens from Indonesia. [Description and figures.]

——— Ramadan, 1936. Bull. Fac. Sci. Egypt. Univ. 6: 13; 1 specimen from the Red Sea.

——— Barnard, 1946. Ann. Mag. Nat. Hist. XI, 13: 388; specimen from Natal, South Africa. [Locality only.]

——— Barnard, 1950. Ann. S. Afr. Mus. 38: 731, figs. 137 a–d; 1 specimen from Natal, South Africa. [Partial redescription.]

Athanas orientalis Pearson, 1905. Rep. Pearl Fish. Maanar 4(24): 88, pl. 2, fig. 10; 7 specimens from Ceylon.

Athanas haswelli Coutière, 1908. Bull. Soc. Philom. Paris IX, 11(5): 2; 1 female from south Adelaide coast, Australia.

——— Hale, 1927. Crustacea of South Australia. Vol. 1. P. 47. [Brief remarks, no additional specimens.]

Athanas granti Coutière, 1908. Bull. Soc. Philom. Paris IX, 11(5): 192; 5 specimens from south Adelaide coast, Australia.

——— Hale, 1927. Crustacea of South Australia. Vol. 1. P. 47. [Brief remarks, no additional specimens.]

Athanas sibogae de Man, 1910. Tijdschr. Ned. Dierk. Ver. II, 11(5): 314; 9 specimens from Indonesia.

——— de Man, 1911. Siboga Exped. $39a^1$(2): 151, pl. 2, figs. 6–6h. [Redescription, same specimens as the above.]

Athanas tenuipes de Man, 1910. Tijdschr. Ned. Dierk. Ver. II, 11(5): 316; 1 specimen from Indonesia.

——— de Man, 1911. Siboga Exped. $39a^1$(2): 157, pl. 3, figs. 8–8e. [Redescription, same specimen as the above.]

Athanas parvus de Man, 1910. Tijdschr. Ned. Dierk. Ver. II, 11(5): 315; 1 female from Indonesia.

——— de Man, 1911. Siboga Exped. $39a^1$(2): 148, pl. 1, figs. 4–4d. [Redescription of same specimen.]

——— Tattersall, 1921. J. Linn. Soc. Lond. 34: 372; 3 specimens from the Red Sea. [Brief remarks.]

——— de Man, 1922. Siboga Rep. $39a^4$(5): 16–18; 1 specimen from Indonesia. [Complete description.]

——— Kubo, 1940. Annot. Zool. Jap. 19(2): 99, figs. 1, 2; 1 specimen from Tanabe, Wakayama Prefecture. [Redescription.]

——— Miyadi, 1940. Annot. Zool. Jap. 19(2): 143. [Same specimen as reported by Kubo above.]

Athanas jedanensis de Man, 1910. Tijdschr. Ned. Dierk. Ver. II, 11(5): 313; 4 specimens from Indonesia.

——— de Man, 1911. Siboga Exped. $39a^1$(2): 154–156, pl. 2, figs. 7–7f. [Redescription of same specimens.]

Athanas grimaldii Coutière, 1911. Bull. Inst. Océanogr. Monaco No. 197, figs. 1–6. [Not Indo-Pacific.]

Athanas polymorphus Kemp, 1915. Indian Mus., Mem. 5(3): 289, figs. 31, 32; 27 specimens from Chilka Lake, India.

Athanas sp. Stebbing, 1914. Ann. S. Afr. Mus. 15: 88; 1 specimen from Delagoa Bay, Indian Ocean.

Athanas stebbingi de Man, 1920. Zoöl. Meded. 5(3): 106; 1 specimen from Indonesia.

——— de Man, 1922. Siboga Exped. $39a^4$(5): 18, pl. II, III, figs. 10–10f. [Redescription of same specimen.]

Athanas crosslandi Tattersall, 1921. J. Linn. Soc. Lond. 34: 372, pl. 27, figs. 13–17; 2 specimens from the Red Sea.

——— Ramadan, 1936. Bull. Fac. Sci. Egypt. Univ. 6: 12; specimen from the Red Sea. [Included in species listing.]

Athanas gracilis Boone, 1935. Bull. Vanderbilt Oceanogr. (Mar.) Mus. 6: 122–126, pl. 32; 1 specimen from Raiatea Island, Society Archipelago.

Athanas japonicus Kubo, 1936. J. Fish. Inst. Tokyo 31(2): 43, pl. 13; 3 specimens from Japan.

Athanas oshimai Yokoya, 1936. Jap. J. Zool. 7: 129, fig. 1; several specimens from Aburatubo, Japan.

Athanas erythraeus Ramadan, 1936. Bull. Fac. Sci. Egypt. Univ. 6: 13, pl. 1, fig. 1; 1 specimen from Ghardaqa, Red Sea.

Athanas esakii Kubo, 1940. J. Fish. Inst. Tokyo 34(1): 93, fig. 13; four specimens from Kusaie, Caroline Islands.

Athanas lamellifer Kubo, 1940. Annot. Zool. Jap. 19(2): 102–106; figs. 3–5; 4 specimens from Kominato, Japan.

Athanas kominatoensis Kubo, 1942. Zool. Mag. Tokyo 54: 82–84, fig. 2; 5 males from Kominato, Japan.

Athanas nouvelae Holthuis, 1951. Atlantide Rep. (2): 104–110, fig. 22. [Not Indo-Pacific.]

Athanas amazone Holthuis, 1951. Atlantide Rep. (2): 111, fig. 23. [Not Indo-Pacific.]

Athanas setoensis Kubo, 1951. J. Tokyo Coll. Fish. 38(2): 265, figs. 5, 6; 1 specimen from central Japan.

Athanas marshallensis Chace, 1955. Proc. U. S. Nat. Mus. 105(3349): 17–20, fig. 8; 22 specimens from the Marshall Islands.

——— Banner, 1957. Pacif. Sci. 11(2): 193, fig. 3 a–f; 1 specimen, Marshall Islands.

Athanas dubius Banner, 1956. Pacif. Sci. 10(3): 322–325, fig. 2 a–h; 10 specimens from Saipan, Mariana Archipelago.

Arete dorsalis Stimpson, 1861. Proc. Acad. Nat. Sci. Philad. 12: 32; found near Hong Kong. [Nec. *A. dorsalis* de Man (1888: 527), see *A. amboinensis*.]

——— Coutière, 1896. Bull. Mus. Hist. Nat., Paris 2: 385; 1 specimen from Samoa and 1 from the Indian Ocean. [Brief description.]

——— Coutière, 1897. Bull. Mus. Hist. Nat., Paris 3(6): 234; several specimens from Djibouti. [Remarks on ecology.]

——— Coutière, 1903. Bull. Soc. Philom. Paris IX, 5(2): 13, figs. 32–34. [States *A. dorsalis pacificus* Coutière is a synonym of *A. dorsalis*.]

——— Coutière, 1905. Fauna and Geog. Maldive and Laccadive Archipelagoes 2(4): 866, figs. 136–137; 1 specimen from Goidu Atoll, Indian Ocean.

——— Chilton, 1910. Trans. Proc. N. Z. Inst. 43: 549; 3 specimens from Sunday Island, Kermadec Islands. [Description of specimens.]

——— de Man, 1911. Siboga Exped. $39a^1$ (2): 167; 2 females from Indonesia. [Description of specimens.]

——— Gee, 1925. Lingnaam Agric. Rev. 3: 157; specimens from China. [Record of capture.]

——— Gordon, 1935. Ann. Mag. Nat. Hist. X, 16: 629; specimens from Christmas Island, Indian Ocean. [Record of capture.]

Arete monoceros Paulson, 1875. Crustacea Mer Rouge. [Paper not available; Coutière, 1899: 27, states this is *Athanas monoceros* (Heller).]

Arete mascarenicus (Richters), 1880. (As *Athanas mascarenicus*), Beitr. Meeresfauna der Insel Mauritius und der Seychellen, Decapoda, p. 164; Indian Ocean.

——— Coutière, 1897. Bull. Mus. Hist. Nat., Paris (7): 301. [Brief remarks.]

——— Coutière, 1899. Ann. Sci. Nat. VIII, Zool. 9: 33. [States this is a synonym of *A. dorsalis*.]

Arete borradailei Coutière, 1903. Bull. Soc. Philom. Paris IX, 5(2): 80; 1 specimen from the Maldive Archipelago.

——— Coutière, 1905. C. R. Acad. Sci., Paris 140: 737. [Listing of specimens in the Maldive Archipelago.]

——— Coutière, 1905. Fauna and Geog. Maldive and Laccadive Archipelagoes 2(4): 861, fig. 133. [Same specimens as in 1903 above.]

Arete dorsalis pacificus Coutière, 1903. Bull. Soc. Philom. Paris IX, 5(2): 84, figs. 31–34; found in Hong Kong, has specimens from Samoa, New Caledonia, and Central America. [Coutière (1905: 866) states this is probably *A. dorsalis* Stimpson.]

——— Coutière, 1904. Bull. Mus. Hist. Nat., Paris 10(2): 58; several specimens from Marutea, Tuamotus. [Notes on commensalism; in 1905 Coutière names this form *A. maruteensis*.]

Arete dorsalis indicus Coutière, 1903. Bull. Soc. Philom. Paris IX, 5(2): 84; several specimens from Djibouti, one from the Maldive Archipelago. [Changed to *A. indicus* by Coutière (1905: 863), see below.]

Arete maruteensis Coutière, 1905. Bull. Mus. Hist. Nat., Paris 11(1): 18; 3 examples from

Marutea commensal with *Heterocentrotus mammillatus.*

——— Coutière, 1905. Fauna and Geog. Maldive and Laccadive Archipelagoes 2(4): 868. [Comparison with *A. dorsalis.*]

——— Nobili, 1907. Mem. R. Accad. Torino II, 57: 353; 5 specimens from Marutea, one from Fakarawa, one from Rikitea, French Oceania. [Remarks on commensalism.]

Arete indicus Coutière, 1905. Fauna and Geog. Maldive and Laccadive Archipelagoes 2(4): 863, figs. 134, 135; one specimen from Maldive Archipelago, numerous specimens from Djibouti and 1 from Central America. [See *A. dorsalis indicus* Coutière above.]

——— Nobili, 1906. Bull. Sci. Fr. Belg. 20: 24; 1 specimen from the Persian Gulf. [Partial redescription.]

——— Balss, 1915. Ergebn. Zool. 30: 21; specimens from the Red Sea. [Locality only.]

——— Coutière, 1921. Trans. Linn. Soc. Lond. 17(4): 413; specimens from the Indian Ocean. [Locality only.]

Arete iphianassa de Man, 1910. Tijdschr. Ned. Dierk. Ver. II, 11(5): 312; 2 specimens from Indonesia.

——— de Man, 1911. Siboga Exped. $39a^1(2)$: 16, pls. 3, 4, figs. 11–11e. [Same as the above with figures.]

——— de Man, 1922. Siboga Exped. $39a^4(5)$: 22, pl. III, figs. 11–11f; 1 specimen from Indonesia. [Redescription.]

——— Banner, 1956. Pacif. Sci. 10(3): 324; 6 examples from the Marianas Islands. [Locality only.]

Arete maruteensis Coutière var. *salibabuensis* de Man, 1910. Tijdschr. Ned. Dierk. Ver. II, 11(5): 313; 1 female from Salibabu Island, Indonesia.

——— de Man, 1911. Siboga Exped. $39a^1(2)$: 169, fig. 13 a–c. [Same specimens as the above, with plates.]

Arete amboinensis de Man, 1910. Arch. Naturgesch. 76(1): 25, figs. 1–6; 1 example from Amboina.

Arete intermedius Yu, 1931. Bull. Mus. Hist. Nat., Paris 3(6): 513, fig. 1; one specimen from Amoy, China.

Arete ghardaqensis Ramadan, 1936. Bull. Fac. Sci. Egypt. Univ. 6: 15, pl. 1, fig. 208; 5 specimens from the Red Sea.

Athanas AND *Arete*

According to Coutière's monograph (1899: 322 *et seq.*) the principal differences between *Athanas* and *Arete* lie in the carpus of the second legs, five-jointed in *Athanas* and four-jointed in *Arete;* in the biunguiculation of the dactylus of the third leg in *Arete,* simple in *Athanas;* and in the branchial formula, which contains only six epipodites in *Arete* and seven in *Athanas.* The other differences he cited were mostly differences in proportion, not form. ("Antennules et antennes d'*Athanas,* mais massives et courtes.") With his description of *Athanas areteformis* Coutière felt he had a specimen that showed transition between the two genera. Subsequent description of species by various authors extended the knowledge of differences in form within the two genera, especially in *Athanas,* which, for example, was found to include species with a biunguiculate dactylus.

The two genera have continued to be accepted as separate in spite of the fact that *Athanas areteformis* on one hand and *Arete borradailei* and, later, *Arete ghardaqensis,* on the other hand, lie in a position somewhat intermediate between the two genera. They were still separated on the basis of the carpus of the second legs and on the branchial formula.

This is in spite of the fact that in other genera it has been recognized that the branchial formula varies within a genus, for example in *Betaeus* and *Alpheopsis,* and that the number of carpal articles of the second legs may also vary as in *Alpheopsis* and *Synalpheus.* Kemp (1915: 295) in his description of *Athanus polymorphus* reported that in his specimens the number of carpal articles varied from four to five.

In the present study, the branchial formula of *Athanas djiboutensis* was examined in 17 specimens from one locality on Canton Island, Phoenix group. Because the species is small and the branchial formula is difficult to discern, most specimens were examined on both sides. Only two of the specimens had mastigobranchs on the third thoracic appendages and the setobranchs on the fourth, the branchial formula for the genus; on the other 15 specimens the last mastigobranch was on the second maxilliped and the last setobranch (at least in those specimens where it was large enough to be seen) was on the third maxilliped. The two specimens with the more complete set did not differ in any other way from the specimens with the reduced branchial formula. Other specimens from Canton and from other localities were spot checked; most were found with the reduced formula, but occasional individuals carried the more complete set. Thus the more common branchial formula in *Athanas djiboutensis* is the same as that for *Arete.*

Athanas verrucosa Banner, described below, is definitely related to the species known as *Arete borradailei* and *Arete ghardaqensis* in the form of the rostrum, in the form of the large chela, which is unlike those found in other species of either *Athanas* or *Arete,* and in the general configuration of the body and appendages. In fact, even the specific distinctions between these nominal species is in doubt. However, the second legs of *Arete borradailei* and *Arete ghardaqensis* have the four-jointed carpus while *Athanas verrucosa* a five-jointed carpus. It would be unacceptable to place such closely related species in separate genera.

The distinctions, therefore, between *Athanas* and *Arete* have been entirely lost, and *Arete* must be regarded as a synonym of *Athanas.* Further supporting the combination of the two genera is the fact that species in both genera show parallel variation in the form of the large chela with sex and maturity.

Athanas

REDEFINITION: Alpheidae in which the rostrum is well developed; supra-, extra- and infracorneal spines usually present with varying degrees of development; corneas of eyes exposed anteriorly and largely dorsally and laterally; chelae of the first legs well developed, either carried extended or flexed against an expanded merus, usually asymmetric and sexually dimorphic, always without the cylinder and plunger characteristic of *Alpheus;* carpus of second legs with four or five articles; dactylus of third legs simple or bifid; pleura of sixth abdominal segment articulated; telson without anal tubercles, tip arcuate. Branchial formula variable.

DIAGNOSIS: The exposure of the eyes and the form of the large chela separate this genus from *Alpheus, Thunor,* and *Synalpheus;* the articulation of the sixth pleura from *Pterocaris, Automate, Salmoneus, Amphibetaeus, Betaeus* (in part), *Batella, Metabetaeus, Racilius,* and *Pomognathus.* The presence of a rostrum separates the genus from *Betaeus* and *Parabetaeus,* and the exposure of the eyes in dorsal view from *Alpheopsis, Neoalpheopsis* and *Athanopsis.* Finally the lack of high dorsal and ventral keel on the rostrum separates this genus from *Aretopsis.*

TYPE SPECIES: *Palaemon nitescens* Leach, 1814.

VARIATION IN FORM

Because previous workers usually had only a few specimens of each nominal species, most were unaware of the variation that might occur. In the present collections the following species are present in great enough numbers to at least tentatively delimit the extent of variation: *A. areteformis* Coutière, *A. parvus* de Man, *A. djiboutensis* Coutière, *A. marshallensis* Chace, *A. rhotionastes* Banner, *A. dorsalis* (Stimpson), and *A. indicus* (Coutière). Of these only one species, *A. djiboutensis,* the most widespread species both ecologically and geographically, seems to show no marked variation except in the branchial formula, as discussed above, and in the chela. In specimens of this species the form of the rostrum, the teeth about the orbits, and the legs are quite constant. The chelae do show changes in proportion with maturity and sex, but these differences are more slight than in other species. The other species all show marked variation. It is the chelae that have the greatest variation. For example, in the two closely related species, *A. marshallensis* and *A. rhothionastes,* the chelae in the females start out as slender appendages where the merus is not expanded, the palm scarcely broader than the merus, the carpus almost as long as the palm; in this condition the fingers are straight and unarmed (Fig. 2). As the individual grows larger the merus expands to accommodate the chela; the palm grows heavy, the fingers develop strong teeth, the carpus either remains the same length, shortening in relation to adjacent articles, or becomes shorter by actual measurement. In the males a comparable but greater differential growth occurs, so that the fully developed male chela is much heavier than that of the female, with a broader merus and palm, a shorter carpus, and with much heavier teeth on the fingers. In *A. dorsalis* it was found that chelae of the smaller males approached the form of the more mature females, and, in one case, the chela of an extremely large female was quite similar to the normal large males (Fig. 5*e*). This variation was not found to be perfectly correlated with size or maturity; for example, females with a definitely "immature" type of chela were found to be ovigerous, and specimens of the same size from the same locality were found to be of varying development. On all species represented with a sufficient number of specimens this variation was observed, with only *A. djiboutensis* showing it to a more minor extent.

A variation somewhat similar to this was noted by Kemp (1915: 289 *et seq.*) for the males of his species *A. polymorphus.* He had a limited number of specimens and came to the conclusion that breeding activity, not growth, caused the polymorphism. We believe that the evidence given in the following pages indicates that the "polymorphism" must stem primarily from growth. Kemp was also unaware that his variation could be found in other species but he cautioned ". . . it is not unlikely that different forms of the same species have been described under separate names."

More perplexing is the apparent variation in the region of the anterior carapace. In the classification of the species the breadth and length of the rostrum, and the development of supra-, extra- and infracorneal teeth, have been regarded as quite constant and used for specific distinctions. However, in a group of 30 specimens of *A. dorsalis* the tip of the rostrum was found to reach from the end of the first antennular article to the middle of the third antennular article; in the same group of specimens the extracorneal teeth were usually well developed and acute, but in one they were lacking. In *A. areteformis* some specimens carried an infracorneal tooth of varying development, some did not (in three specimens from the same location two are without teeth, the third with a small infracorneal tooth bilaterally developed).

To the contrary *A. marshallensis, A. rhothionastes,* and *A. djiboutensis* all present in some numbers in the collections, are quite uniform in the development of these parts. It would appear that some species are inherently more variable than others, a condition found in members of the genus *Alpheus.*

Finally, in *A. dorsalis* the development of the tooth on the merus of the third legs and the proportions of articles of this leg were also found to vary. Like species in other genera of the family, the telson also varies in its proportions.

These variations will be discussed more fully for each species in the following section.

These variations in parts previously considered to be of taxonomic importance render it difficult to decide upon a valid basis for species differentiation. A possible clue to aid systematists may be found in the ecology of the forms being considered. At least in two pairs of closely related species the most valuable clue is their environment. *A. dorsalis* appears to be usually, if not always, associated with sea urchins of the genus *Heterocentrotus,* while the closely related *A. indicus* with the sea urchins of the genus *Echinometra;* again in the closely related pair, *A. marshallensis* and *A. rhothionastes, A. marshallensis* appears to be found only in the silty sandy shorelines of lagoons, associated with *Alpheus strenuus* Dana (whether it is a symbiotic association or a mere ecological association is not known), while *A. rhothionastes* has been found almost exclusively on the coralline ridge of seaward reefs where it is subjected to heavy surf. This type of aid, however, is also questionable, for *A. djiboutensis* is widespread in its environments; most were collected from either the inner zone of outer reefs on islands, especially on the lee side of an island, or from somewhat similar conditions on the lagoon beaches of an atoll; some, however, were collected from near the surf line.

With so much variation, with the extent of this variation apparently inconstant from species to species, and with so many species described on the basis of one or several individuals, it is impossible to decide which species put into the two genera should be regarded as valid. In the following key we have not combined any species for which we have no specimens. We also do not include the few non-Indo-Pacific species, but we do include those species from the Pacific that are nontropical.

KEY TO THE INDO-PACIFIC SPECIES OF *Athanas*[3]

1. Palm of large chela cylindrical or subcylindrical in section; carpus of second legs with five articles.... 2

Palm of large chela flattened, definitely higher than broad in section, carpus of second legs with four or five articles........................22

2(1). Legs of first pair, when fully developed, carried directed forward; merus short, not excavate............. 3

Legs of first pair, when fully developed, with chelae carried folded against an excavate and expanded merus 6

3(2). Supracorneal teeth present.............. ....*A. areteformis Coutière*[4]

Supracorneal teeth absent................. 4

4(3). Dactylus of third legs biunguiculate.....................**A. granti** Coutière

Dactylus of third legs simple, but may carry an articulated spinule at usual point of biunguiculation.... 5

5(4). Dactylus of third legs simple; with both extra- and infracorneal teeth ....**A. crosslandi** Tattersall

Dactylus of third leg carrying an articulated spinule; with only extracorneal teeth (originally described as infracorneal teeth)...... ....**A. gracilis** Boone

6(2). Supracorneal teeth present.............. ....*A. djiboutensis* Coutière

Supracorneal teeth absent............. 7

7(6). Dactylus of third leg biunguiculate.. 8

Dactylus of third leg simple........ 9

8(7). With infracorneal tooth.................. ....*A. parvus* de Man

Without infracorneal tooth or projection..........**A. jedanensis** de Man

9(7). Carpus of first leg longer than palm in mature females.......................10

Carpus of first legs equal in length to palm, or shorter, in mature females 15

10(9). Ischium of first legs with strong distal spine........**A. orientalis** Pearson

Ischium of first legs not so armed....11

11(10). Palm of chela in female less than 1.5 times length of fingers..........12

Palm of chela in female 2.0 or more times length of fingers................13

12(11). Palm of chela in female shorter than fingers; stylocerite reaching to end of third antennular article; dactylus of third legs one-third length of propodus..................... ....**A. setoensis** Kubo

Palm in female equal to fingers; stylocerite reaching slightly past end of first antennular article; dactylus of third legs more than half length of propodus............... ....**A. polymorphus** Kemp

13(11). With extracorneal tooth strong and acute; infracorneal projection almost as long as extracorneal tooth, but rounded...................... ....**A. stebbingi** de Man

With only extracorneal tooth (or infracorneal tooth) produced and acute 14

14(13). Rostrum reaching to end of second antennular article........................ ....**A. dimorphus** Ortmann

Rostrum a little longer than antennular peduncle........................... ....**A. monoceros** (Heller)

15(9). Infracorneal projection at most slight and rounded.......................16

Infracorneal projection present and acute 18

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[3] *Athanas tenuipes* de Man is omitted from the key as the type specimen, the only specimen known, lacked both legs of the first pair. Otherwise, it is characterized by five articles in the carpus of the second legs, the lack of supracorneal teeth, the presence of extra- and infracorneal teeth; its rostrum reaches to the middle of the second antennular article; and third legs and telson of slender and elongate form.

[4] Those species whose names are in italic are discussed in this paper.

16(15). Rostrum reaching to end of antennular peduncle .... **A. lamellifer** Kubo
Rostrum at most reaching to end of second antennular article, usually shorter 17

17(16). Palm of chelae 2.5 times length of carpus, or shorter, in mature females........*A. marshallensis* Chace
Palm of chelae 3 to 5 times length of carpus in mature females.........................*A. rhothionastes* Banner

18(15). Infracorneal tooth longer than extracorneal tooth 19
Infracorneal tooth shorter than extracorneal tooth 20

19(18). Dorsal carina extending along anterior half of carapace and rostrum.................**A. japonicus** Kubo
Anterior carapace without dorsal carina.......................*A. esakii* Kubo

20(18). Dactylus of large chela of male strongly curved, "half-moon shaped," much longer than fixed finger...............**A. oshimae** Yokoya
Dactylus of large chela of male at most slightly curved, not "half-moon shaped," not markedly longer than fixed finger (males unknown in *A. haswelli* below)..21

21(20). Carpus and chelae slender in females[5]............**A. haswelli** Coutière
Carpus and chelae of females more robust[5]....**A. minikoensis** Coutière

22(1). With well-developed supracorneal teeth 23
Without trace of supracorneal teeth; carpus of second legs with four articles 25

23(22). With carpus of second legs with five articles, lower portion of palm of large chela bearing numerous papillae...*A. verrucosus* Banner
With carpus of second legs with four articles; lower portion of palm of large chela without papillae 24

24(23). Ventral side of rostrum smoothly convex; base of outer flagellum with four articles; propodal spine of uropod simple..**A. borradailei** (Coutière)
Ventral side of rostrum with an obtuse angle; base of outer antennular flagellum with more than four articles; propodal spine of uropod bifid ....**A. ghardaqensis** (Ramadan)

25(22). Rostrum reaching to middle or end of third article of antennular peduncle. Usually associated with sea urchins of the genus *Echinometra*........*A. indicus* (Coutière)
Rostrum not reaching past middle of second antennular article, usually only to end of first article or shorter 26

26(25). Telson elongate, 6.5 times as long as posterior margin is broad; posterior margin one-third breadth of base. Symbiotic association, if any, unrecorded..**A. amboinensis** (de Man)
Telson less than 4 times as long as posterior margin is broad; posterior margin one-fourth to one-fifth breadth of base. Usually associated with sea urchins of the genus *Heterocentrotus* ....*A. dorsalis* (Stimpson)

Athanas areteformis Coutière

Athanas naifaroensis Coutière, 1903. Bull. Soc. Philom. Paris IX, 5(2): 77, figs. 14–16; [same description and figures in 1905, Fauna and Geog. Maldive and Laccadive Archipelagoes 2(4): 859, fig. 131 a–c].

Athanas areteformis Coutière, 1903. *Op. cit.* p. 79, figs. 17–19; [same description and figures in 1905, *op. cit.*, p. 860, fig. 132 a–c].

Athanas erythraeus Ramadan, 1936. Bull. Fac. Sci. Egypt. Univ. 6: 13, pl. 1, fig. 1.

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[5] Coutière's only differentiation between these two species is as follows: "[The cheliped of *A. haswelli*] a la même forme cylindrique et grêle [as *A. dimorphus*] ce qui distingue l'espèce de l'*A. minikoensis* où la pince est beaucoup plus robust et le carpe court." Bull. Soc. Philom. IX, 11(5): 2. 1908.

Athanas dubius Banner, 1956. Pacif. Sci. 10(3): 323, fig. 2a–h.

DISCUSSION: These four nominal species were all described on the basis of a few specimens, as listed in the introduction: Coutière had two females, one incomplete, for *A. naifaroensis;* one complete male and one incomplete female for *A. areteformis;* Ramadan had one female for *A. erythraeus;* I had nine specimens from Saipan. Since the original description several more specimens have been reported for *A. areteformis* (Chace, 1955: 21; Balss, 1915: 30) and for *A. naifaroensis* (de Man, 1922: 16; Barnard, 1950: 731) and no more specimens have been reported for *A. erythraeus.*

The four species were separated by various characteristics. *A. naifaroensis* differed from *A. areteformis* seemingly only in the presence of infracorneal spines (the chela of the male had never been observed). For his species, Ramadan listed a number of differences that would distinguish it from *A. areteformis:* 1. The visible portion of the first article of the antennular peduncle he stated was considerably longer than the sum of the other two in *A. areteformis* and about equal to the sum in *A. erythraeus.* Apparently this is in error, for Coutière does not state or show such a relationship, and in specimens that are plainly *A. areteformis* the relationship is as it is described for *A. erythraeus.* 2. The lateral corneal spine "is not as well developed" in *A. erythraeus* as in *A. areteformis.* 3. The chela of the female in *A. erythraeus* is like that of the male *A. areteformis* (although Ramadan's plate does not show this condition); the dactyl and fixed finger had low teeth.

A. dubius was distinguished from *A. areteformis* principally by the forms of the male and female chelae with the fingers on the male being slender and straight more like the female *A. areteformis,* and the palm on the female being broader; also the ischium on the male and female carried spines which apparently were lacking in the female *A. areteformis.*

In the present collections there are 25 specimens that can be referred to this complex; unfortunately, many of them are small or incomplete.

These specimens are found to be variable in all characteristics that have been used for the separation of these species. The rostrum reaches from near the end of the second antennular article to the middle of the third; in some the basal portion has parallel sides, in others the rostrum has an almost uniform taper to the tip. The supracorneal teeth are well developed and acute in some, while in others they are shorter and more rounded, like the condition depicted for *A. dubius;* the cleavage between the base of the rostrum and supracorneal spines also varies in depth and definition. All but five specimens lack the infracorneal tooth; however, on these five the tooth varies from considerably smaller to larger than that depicted for *A. naifaroensis.* In the collection are three specimens from Tonga from the same location, two without teeth and the third carrying a small but definite tooth.

Similar variations can be seen in the length ratios of the antennular articles, and at least within narrow limits, in the development of the lateral spine of the scaphocerite.

In the series many of the specimens lack the chelae. The females all show the type illustrated for *A. naifaroensis* and *A. dubius.* In this appendage the merus varies from 2.5 to 3.3 times as long as broad, with the two sides showing asymmetry and the larger specimens in general with the higher ratios; the length-breadth ratio of the carpus runs from 0.7 to 1.1; the palm, 2.0 to 2.7; the palm varies from 1.3 to 1.8 times the length of the fingers. All specimens have from three to five spines on the ischium. One female of 3.3 mm. carapace length had slight teeth on the dactylus, similar to those described by Ramadan.

Of the males all specimens but one also had a chela as described for *A. dubius* and female of *A. areteformis* with a slender merus, with the length from 1.6 to 3.0 times the breadth; the carpus somewhat elongate, 0.8 to 1.0 times as long as broad; the palm from 1.4 to 2.6 times as long as broad, and the palm 1.4 to 1.8 times the length of the fingers. However, the largest of all males, with a carapace length of 3.2 mm. had the form described for the male *A. areteformis,* with short curved fingers, a heavy cylindrical palm 3.3 times the length of the fingers. This specimen came from the same collection (BE-11) as did two larger females and a small male (carapace length of 2.2 mm.) with a typically

TABLE 1

VARIATION IN PROPORTIONS IN THE CHELAE OF *Athanas djiboutensis* COUTIÈRE

LOCALITY	SEX	CARAPACE LENGTH	SMALL CHELA						LARGE CHELA					
			Fingers (in proportion to palm)	Palm	Carpus	Merus	Merus 1/b	Carpus 1/b	Fingers (in proportion to palm)	Palm	Carpus	Merus	Merus 1/b	Carpus 1/t
Tahiti	♀	2.7 mm.	0.8	1.0	1.0	1.6	—	—	0.4	1.0	0.2	1.0	—	—
Tahiti	♀	2.7 mm.	1.0	1.0	1.4	2.0	1.6	2.3	0.5	1.0	0.2	1.2	3.0	1.2
Tonga	♀	3.0 mm.	0.8	1.0	1.1	1.8	1.7	2.7	0.4	1.0	0.2	0.9	4.0	1.7
Samoa	♀	3.0 mm.	0.7	1.0	0.9	1.5	2.7	2.0	0.4	1.0	0.2	1.2	5.0	1.6
Canton	♀	3.0 mm.	0.8	1.0	2.0	1.8	4.0	4.0	0.4	1.0	0.2	1.0	2.0	—
Samoa	♀	3.4 mm.	0.8	1.0	1.1	2.0	3.5	2.0	0.4	1.0	0.2	1.0	4.3	1.1
Tonga	♀	3.5 mm.	0.7	1.0	1.2	1.6	3.0	2.5	0.3	1.0	0.2	1.0	4.6	1.4
Tonga	♀	3.6 mm.	—	—	—	—	—	—	0.3	1.0	0.2	1.2	4.1	0.7
Samoa	♂	2.1 mm.	0.8	1.0	0.8	1.4	3.5	2.0	0.4	1.0	0.3	1.0	5.2	1.2
Tahiti	♂	2.2 mm.	0.8	1.0	0.9	1.8	3.0	1.5	0.4	1.0	0.4	1.2	3.0	1.1
Tahiti	♂	2.4 mm.	0.7	1.0	0.3	1.2	—	—	0.3	1.0	0.2	1.1	3.0	1.8
Samoa	♂	2.4 mm.	0.6	1.0	0.9	1.6	2.0	1.6	—	—	—	—	—	—
Samoa	♂	2.4 mm.	0.8	1.0	1.1	1.6	2.6	2.0	0.4	1.0	0.2	1.0	2.5	1.1
Tahiti	♂	2.4 mm.	0.8	1.0	1.0	1.6	1.3	2.5	—	—	—	—	—	—
Fiji	♂	2.5 mm.	—	—	—	—	—	—	0.4	1.0	0.3	1.2	2.2	1.0
Eniwetok	♂	2.7 mm.	0.6	1.0	0.3	1.2	2.5	1.4	0.3	1.0	0.3	1.0	2.2	1.0
Eniwetok	♂	2.7 mm.	0.6	1.0	0.6	1.8	2.6	1.6	0.4	1.0	0.3	1.0	2.1	1.0
Eniwetok	♂	2.8 mm.	0.4	1.0	0.3	1.3	3.8	1.0	0.4	1.0	0.2	1.0	2.4	1.0
Samoa	♂	2.8 mm.	0.5	1.0	0.3	1.4	2.8	1.0	0.4	1.0	0.1	1.0	2.3	1.0
Eniwetok	♂	3.1 mm.	0.4	1.0	0.3	0.9	2.4	1.0	0.2	1.0	0.1	0.8	2.9	1.0
Samoa	♂	3.2 mm.	0.5	1.0	0.2	1.3	2.3	0.9	0.3	1.0	0.3	1.1	2.0	1.5
Samoa	♂	3.4 mm.	0.5	1.0	0.2	1.5	2.6	1.0	0.3	1.0	0.2	0.9	2.1	1.1
Samoa	♂	3.6 mm.	0.6	1.0	0.2	1.3	2.3	1.0	0.3	1.0	0.2	0.9	2.1	0.9
Samoa	♂	3.9 mm.	0.6	1.0	0.3	1.3	2.4	1.4	0.3	1.0	0.2	1.0	2.2	1.2

feminine chela. This variation in the chelae is similar to that of other members of the genus.

With these variations the distinctions between the four nominal species have disappeared. As the original description of *A. areteformis* carries the description and figure of the characteristic chela of the male, we have chosen to retain that name rather than the name *A. naifaroensis,* which would have to be selected were strict page priority to be followed.

DISTRIBUTION: These specimens have been reported from South Africa, the Red Sea, the Maldive and Laccadive Archipelagoes, and the Marianas. Specimens in the present collections were collected from various places on reef flats and fronts, lagoons, lee and windward reefs at varying depths. There is one specimen for Fiji, four from Tonga, one from British Samoa, four from the Cook Islands, three from the Society Islands, and five specimens from the Marshall Islands.

Athanas djiboutensis Coutière

Athanas djiboutensis Coutière, 1897. Bull. Mus. Hist. Nat., Paris 3(6):233.

Athanas sulcatipes Borradaile, 1898. Proc. Zool. Soc. Lond., p. 1011, pl. 65, fig. 9.

DISCUSSION: As discussed in the introductory section this widespread and common species is quite constant in its characteristics except for the branchial formula and the growth and sexual differences of the large chela. Some minor differences in length of the rostrum are found, as was discussed for the Saipan specimens (Banner, 1956: 322).

In Table 1 below, the proportions of the male and female chelae are given for specimens taken at random from the collections and arranged according to carapace length. The changes of proportions with sex and growth are clearly shown, and the variation between specimens of nearly the same size does not appear to be from geographical races, but variation of the type that could be found within a single population.

DISTRIBUTION: This species has been previously reported from the Red Sea, Mozambique, Maldive Archipelago, Christmas Island (Indian Ocean), Indonesia, Great Barrier Reef, Mariana Archipelago, Marshall Islands, Wake Island, Ellice Islands, Samoa, Tuamotus, and the Marquesas. In the present collections specimens are from the Caroline Islands, Marshall Islands, Phoenix Islands, Fiji, Tonga, Samoa, Cook Islands and Tahiti.

Athanas parvus de Man
Fig. 1

Athanas parvus de Man, 1910*a*. Tijdschr. Ned. Dierk. Ver. II, 11(2): 315. [Additional description and figures in Siboga Exped. 39a¹ (2): 148, fig. 4a-d.]

Athanas parvus de Man, Kubo, 1940*b*. Annot. Zool. Jap. 19(2): 99, figs. 1, 2. [Additional description.]

Athanas sibogae de Man, 1910*a*. Tijdschr. Ned. Dierk. Ver. II, 11(2): 314. [Additional description and figures in Siboga Exped. 39a¹ (2): 151, fig. 6a–h.]

DISCUSSION: Unfortunately, none of our eleven specimens are complete. The carapace and the intact appendages agree well with the published descriptions of *Athanas parvus*. There are the usual slight differences in proportions—for example, the merus of the third legs usually runs about 5 times as long as broad instead of 7—but these differences, like those given by Kubo, appear to be of no taxonomic importance.

One male only had a chela intact; it is not known whether this is the larger or smaller, or if they are of symmetrical development. However, as the chela of the male has never been described, it is shown in Figure 1. In it the ischium is rather long and slender; the merus is 3.4 times as long as broad, excavate along the lower margin to accommodate the chela when flexed; the carpus is short and not distally expanded; the palm is slender and tapering, 2.5 times as long as broad, without grooves or ridges; the dactylus has been broken, but the remaining portion of it and the fixed finger are quite straight and bear a series of low, conical teeth. Presumably this is not the fully mature stage of the chela, and in this condition it resembles the chela described for *A. jedanensis* de Man.

A. parvus was previously placed into the Nitescens group of the genus because the chela described for the female, which may be immature, were carried extended; this male shows that its rightful position is in the Dimorphus group. With this differentiating character removed only very slight differences can be found between this species and *A. sibogae*. There is a slight difference in the infracorneal tooth, the chelae appear to be different and the lower unguis of the dactylus of the third leg is heavier and make a greater angle to the dactylus in this species than it does in *A. sibogae*. With the great differences in other species, especially in *A. areteformis*, in the development of the orbital teeth, and with the growth and sex differences in the chela in this genus, the first two characteristics cannot be regarded as sufficient for specific separation; the difference in development of the dactyls is so slight that that too cannot be relied upon. The two species later may be found to be distinct, but with the present knowledge of inherent variation within this

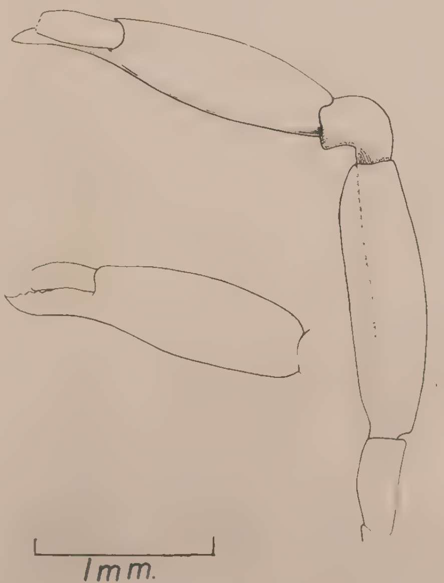

FIG. 1. *Athanas parvus* de Man. Chela of male from Samoa (BBS-10); tip of dactylus lost in specimen.

TABLE 2

VARIATIONS IN THE CHELAE OF *Athanas marshallensis* CHACE

SEX	CARAPACE LENGTH	LEFT CHELA						RIGHT CHELA					
		Fingers	Palm	Carpus	Merus	Merus 1/b	Palm 1/b	Fingers	Palm	Carpus	Merus	Merus 1/b	Palm 1/b
		(in proportion to palm)						(in proportion to palm)					
♀	3.1 mm.	0.6	1.0	1.0	1.4	4.0	2.7	0.5	1.0	1.1	1.5	3.7	2.5
♀	3.5 mm.	0.5	1.0	0.8	1.2	3.8	3.0	0.4	1.0	0.6	1.2	3.8	3.6
♀	3.6 mm.	0.5	1.0	1.0	1.4	4.0	3.4	0.4	1.0	0.6	1.2	4.0	3.3
♀	3.7 mm.	0.3	1.0	0.9	1.3	4.5	3.5	0.3	1.0	0.8	1.3	3.8	2.8
♀	4.5 mm.	0.3	1.0	0.4	1.0	3.0	3.0	0.3	1.0	0.6	1.1	3.3	3.7
♀	4.6 mm.	0.4	1.0	0.8	1.4	3.5	3.1	0.3	1.0	0.6	1.2	3.2	3.4
♀	5.2 mm.	0.4	1.0	0.4	1.1	3.3	3.1	0.4	1.0	0.4	0.9	3.0	3.2
♂	4.3 mm.	0.3	1.0	0.2	0.9	3.0	2.7	0.2	1.0	0.2	0.9	2.8	3.0
♂	4.6 mm.	0.2	1.0	0.2	0.9	2.5	3.0	0.2	1.0	0.2	0.9	2.5	3.0
♂	5.3 mm.	0.3	1.0	0.3	1.0	2.7	2.3	0.3	1.0	0.2	0.9	2.5	3.2

genus, it appears wiser to place *A. sibogae* in synonymy.

Indeed, *A. jedanensis* may also be found to be a synonym. In this species the chief distinction, when the differences in the chelae are ruled out, is the absence of the infracorneal spine. If this is variable, as it is in *A. areteformis,* then there is but one species. However, as in this small collection no transitional forms were found, *A. jedanensis* has been retained.

DISTRIBUTION: *A. parvus* has been reported from the type locality, in Indonesia, and from southern Japan; *A. sibogae* only from Indonesia. Specimens in the present collections came from various places on the reef flats in from 1 to 6 feet of water and were largely from dead coral heads. There were seven specimens from Tonga, and four from Samoa.

Athanas marshallensis Chace

Fig. 2

Athanas marshallensis Chace, 1955. Proc. U. S. Nat. Mus. 105(3349): 17–20, fig. 8.

DISCUSSION: All the 11 specimens available were collected in a single narrow habitat at Eniwetok, Marshall Islands, under loose coral boulders resting on a sandy substrate in the intertidal zone where they were collected together with *Alpheus strenuus* Dana, *Salmoneus tricristatus* Banner, and *S. sibogae* (de Man). It is noteworthy that in similar habitats in other archipelagoes producing widespread *A. strenuus* this species was not collected; all specimens known have been collected solely from the northern Marshall Islands.

In this series of specimens the usual changes in form of the chelae with size and sex are found. Table 2 gives the changes in proportion with size of all specimens collected; Figure 2*b–d* shows the changes with growth in the female and the chela of a mature male for contrast. The proportions show that the chelae of the large male are quite symmetrical; it is possible that the chelae of very large females, larger than those represented in the collection, may also become symmetrical.

The differences between this species and *A. rhothionastes* Banner are discussed under the latter species. This species may prove to be a synonym of *A. esakii* Kubo but at present the two forms appear to be distinct; this is discussed under *A. esakii.*

DISTRIBUTION: As stated above all specimens of this species have been collected from the northern Marshall Islands.

Athanas rhothionastes sp. nov.

Fig. 3

TYPE SPECIMENS: Holotype, a 12 mm. (4.8 mm. carapace length) ovigerous female; allotype, a male of the same size; paratypes from the same locality, at end of surge channels, edge of reef front, leeward (western) side, Canton

Island, Phoenix group, collected by A. H. Banner 1 March 1954. Additional specimens from Eniwetok, Vitilevu, Tongatabu, Opolu, Tutuila, Aitutake, and Tahiti, all from surf zone on reef fronts except for one specimen from the lagoon at Eniwetok (BE-2); this, however, must have been subject to surge for it came from the base of *Pocillopora meandrina* Verrill, a coral that never lives in still waters.

DESCRIPTION: Rostrum acute with sides of uniform taper or with slight "jog" in lateral margins anterior to eyes; tip reaching to middle of second antennular article; slight carina in anterior half. Supracorneal teeth lacking; extracorneal teeth acute, reaching almost to end of corneas; infracorneal projection short and rounded; pterygostomial corner rounded. Corneas of eyes concealed in posterior portion and laterally by extra- and infracorneal projections.

Antennular peduncle short and heavy, with first, second and third articles subequal in length, second article as broad as long. Stylocerite long, lanceolate, tip reaching to near end of third antennular article. Scaphocerite broad and long, tip reaching beyond end of antennular peduncle; lateral spine strong, slightly exceeding squamous portion in length. Basicerite unarmed. Carpocerite reaching about to end of antennular peduncle.

Chelae of large female symmetrical. Ischium bearing four strong spines on superior margin. Merus 3.2 times as long as broad, unarmed; superior external and internal surfaces smooth and flat; inferior surface deeply excavate to accommodate propodus, short, 0.2 to 0.3 length of palm (depending upon place measured), normally greatly flexed. Palm subcylindrical, 3.5 times as long as broad, equal in length to merus, tapering slightly towards fingers; dactylus curved, one-quarter as long as palm with irregular, large rounded teeth matching exactly with teeth on fixed finger. Chelae in allotype of same carapace length considerably larger and slightly asymmetrical with the right almost 10 per cent larger than the left; in both male chelae, merus and palm are markedly thicker than those of the female. Armature of fingers poorly developed in smaller chela; on large chela fixed finger bearing single large rounded tooth and smaller tooth proximally, dactylus bearing two teeth in

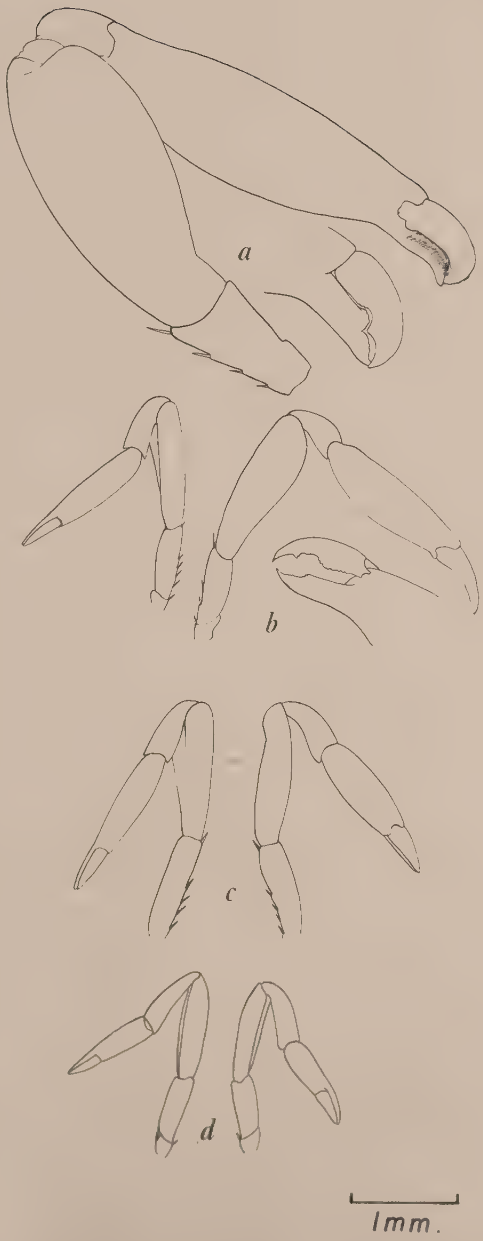

FIG. 2. *Athanas marshallensis* Chace. Chelipeds of various individuals from Eniwetok. *a*, 4.6 mm. ♂; *b*, 4.5 mm. ♀; *c*, 3.7 mm. ♀; *d*, 3.1 mm. ♀. (All to same scale.)

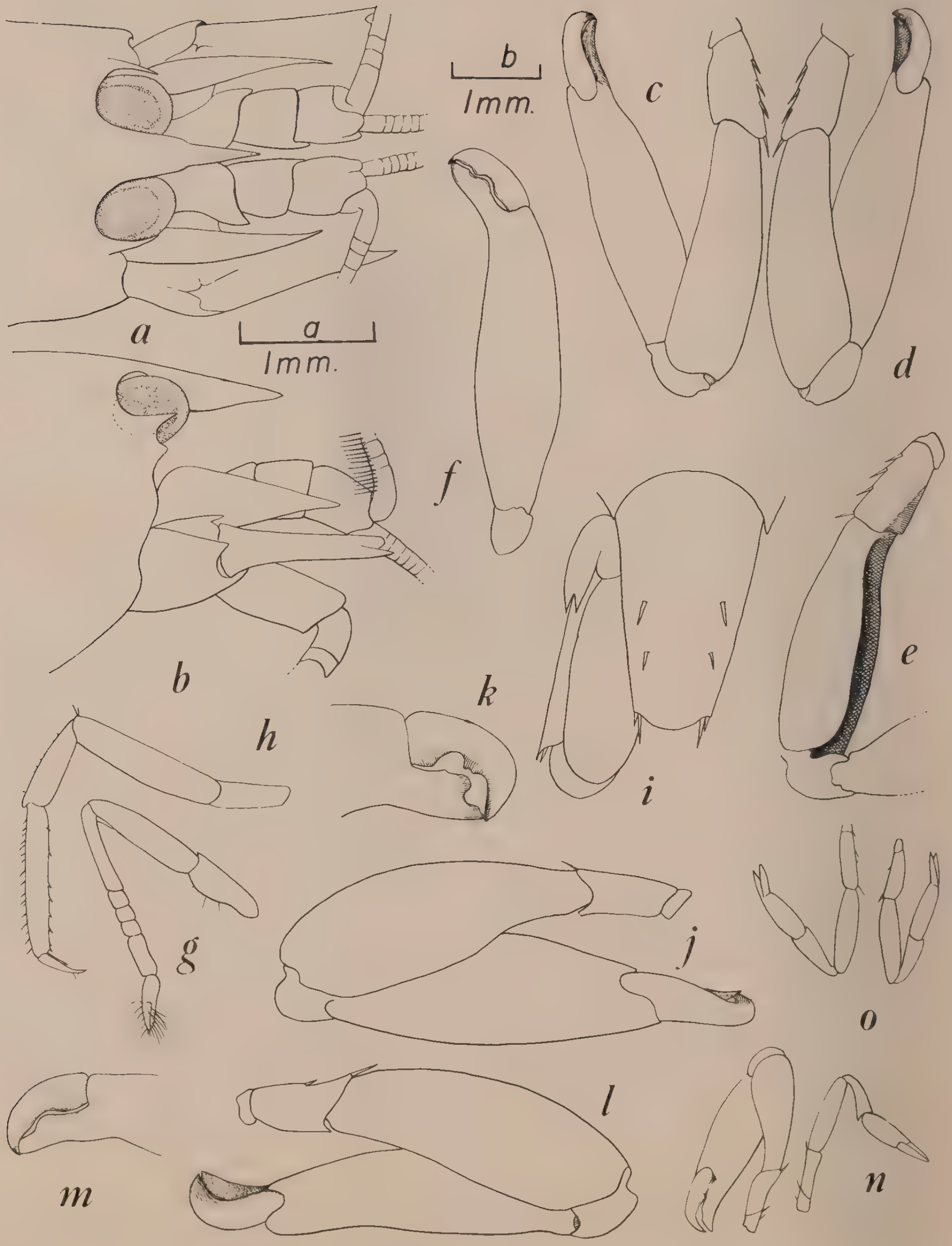
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TABLE 3
VARIATION IN THE CHELIPEDS OF *Athanas rhothionastes* SP. NOV.

LOCALITY	SEX	CARAPACE LENGTH	SMALL CHELA							LARGE CHELA						
			Fingers (in proportion to palm)	Palm (in proportion to palm)	Carpus (in proportion to palm)	Merus (in proportion to palm)	Palm 1/b	Carpus 1/b	Merus 1/b	Fingers (in proportion to palm)	Palm (in proportion to palm)	Carpus (in proportion to palm)	Merus (in proportion to palm)	Palm 1/b	Carpus 1/b	Merus 1/b
Tahiti	♀	2.8 mm.	0.5	1.0	1.6	1.4	2.7	2.5	3.2	0.4	1.0	0.2	0.8	2.7	1.2	2.8
Tahiti	♀	3.2 mm.	0.3	1.0	0.2	1.0	2.6	1.3	2.5	0.4	1.0	0.2	0.8	2.7	1.2	2.5
Tahiti	♀	3.4 mm.	—	—	—	—	—	—	—	0.4	1.0	0.2	1.0	2.8	1.5	2.8
Canton	♀	3.8 mm.	0.3	1.0	0.2	0.8	2.9	1.2	2.8	0.4	1.0	0.2	1.0	3.1	1.4	3.2
Canton	♀	3.9 mm.	0.3	1.0	0.2	0.8	3.0	1.3	3.0	0.3	1.0	0.2	0.9	2.8	1.1	3.6
Eniwetok	♀	4.1 mm.	0.4	1.0	0.2	0.9	2.7	1.4	2.9	0.3	1.0	0.2	0.9	2.6	1.5	2.7
Canton	♀	4.3 mm.	0.4	1.0	0.2	1.0	2.7	1.3	2.7	—	—	—	—	—	—	—
Canton	♀	4.5 mm.	0.4	1.0	0.3	1.1	2.6	1.8	2.8	—	—	—	—	—	—	—
Samoa	♂	2.7 mm.	—	—	—	—	—	—	—	0.4	1.0	0.3	1.1	2.8	1.8	3.2
Tahiti	♂	2.8 mm.	0.3	1.0	0.3	1.0	3.0	1.5	2.7	0.4	1.0	0.2	0.9	2.5	1.0	2.5
Fiji	♂	3.2 mm.	—	—	—	—	—	—	—	0.2	1.0	0.2	0.9	3.0	1.6	2.4
Tonga	♂	3.4 mm.	0.3	1.0	0.2	0.9	2.9	1.6	2.6	0.3	1.0	0.2	0.9	2.6	1.6	2.9
Canton	♂	3.4 mm.	0.4	1.0	0.2	1.0	2.8	1.5	3.3	0.3	1.0	0.2	0.9	2.9	1.3	2.5
Tahiti	♂	3.5 mm.	0.3	1.0	0.1	0.9	3.2	1.6	3.0	—	—	—	—	—	—	—
Tahiti	♂	3.7 mm.	0.3	1.0	0.2	1.1	2.7	1.0	2.9	0.3	1.0	0.2	1.0	3.1	1.2	2.8
Canton	♂	4.2 mm.	—	—	—	—	—	—	—	0.2	1.0	0.2	0.9	3.1	1.0	2.1
Canton	♂	4.3 mm.	0.3	1.0	0.2	1.0	3.0	1.5	2.4	0.3	1.0	0.2	0.9	2.5	0.9	2.4

opposition to large tooth (evidently these are thin and used for cutting as they slide past each other).

Carpal articles of second leg with ratio: 10: 1: 1: 1: 5.

Ischium of third legs unarmed, 0.4 as long as merus; merus unarmed, 5 times as long as broad; superior distal margin of carpus projecting but rounded, carpus 0.5 as long as merus; propodus 0.9 as long as merus, armed with scattered spines along inferior margin; dactylus slender, slightly curved, acute and simple, and 0.3 as long as propodus.

Telson 3.3 times as long as broad distally, twice as broad proximally as distally; lateral margins with uniform taper; tip broadly arcuate; dorsal and terminal spinules normal. Uropods longer than telson, outer uropod armed with tooth and movable spine at articulation.

Color in life not noted.

DISCUSSION: Variation in this series of specimens has been carefully studied to determine if they are distinct from closely related species. The rostrum is always acute, almost always tapering, although there are a few with straight parallel sides in the proximal third to half; the tip reaches from the middle to the end of the second antennular article except for a very small specimen from Samoa, where the tip reaches to the middle of the third antennular article. In many, the rostrum appears more narrow than in the holotype and often has a slight upturn towards the tip when seen in side view. Likewise, with few exceptions, the extra- and infracorneal projections are quite uniform; in the small specimens from Samoa assigned to this species the infracorneal tooth is almost acute; in one from the type locality the extracorneal tooth is bifid on one side and with the infracorneal projection rounded but on the other side in the same specimen the upper tooth is normal and the infracorneal tooth is acute.

FIG. 3. *Athanas rhothionastes* Banner. Holotype (female) *a-i;* allotype *j-m. a. b.* Anterior region; *c. d. e. f.* chelipeds; *f.* interior lateral surface of chelae; *g.* second leg; *h.* third leg; *i.* telson; *j. k.* large cheliped and fingers, *l. m.* small cheliped and fingers; *n.* large and small chelae of 2.7 mm. (carapace length) ovigerous female from Tahiti (BD-2); *o.* same from 3.0 mm. ovigerous female from Eniwetok (BE-4). (Anterior body region and telson, scale a; all other appendages scale b.)

The proportions of the chelipeds are given in Table 3. The 2.7 mm. female from Tahiti with the asymmetrical chela (Fig. 3*n*) is almost certain to belong to this species, for it was collected with larger specimens of the species with normal chelae. There may be some question about the 3.0 mm. female from Eniwetok (Fig. 3*o*) for it was collected alone and its rostrum had been broken. However, as its chelae could represent an earlier stage of development, as it agrees with the species on other characteristics, and as it was collected from the typical habitat of this species, we believe we can safely assume it to belong to *A. rhothionastes*. The development of ischial spines of the chelipeds appears to be variable.

If these two smallest specimens given in the table do belong to this species, then here again we have the variation on the chelipeds with age and sex that seems to be characteristic of so many species of this genus. The degree of uniformity in the rostrum and corneal spines casts some doubt upon the uniting of species like *A. naifaroensis* and *A. areteformis* (see previous sections).

A. rhothionastes is closely related, morphologically, to two species, *A. lamellifer* Kubo and *A. marshallensis* Chace. This group of species of the Dimorphus group are characterized by the lack of supracorneal teeth, acute extracorneal teeth, rounded infracorneal teeth, with the palm definitely longer than the carpus in mature females, and with simple dactyli of the third legs. The distinction between this species and *A. lamellifer* is fine and questionable, for the chief differences lie in the length of the rostrum, which exceeds the length of the antennular peduncle in *A. lamellifer* and usually reaches only to the end of the second antennular article in *A. rhothionastes*, and in the armature of the fingers of the large chela of the male, bearing merely setae in Kubo's species and bearing heavy teeth and setae in this species. The ischium of the cheliped of *A. rhothionastes* appears consistently longer than that reported by Kubo. The carpus of the cheliped is consistently longer in *A. marshallensis* than in *A. rhothionastes* in the immature stages and in the fully developed females; there are no obvious differences between the males of the two species.

Possibly better than the morphological differentiation between the three species would be the ecological differences. *A. rhothionastes* so far as had been collected always occurs in regions of surge or heavy surf on coral reefs, usually on the outermost reef fronts in the coralline ridge and near the end of the surge channels; *A. lamellifer* has been reported only from the colder waters of Tokyo Bay (Tiba Prefecture of Kubo is now transliterated Chika) under stones on a muddy shore, and while there was nothing in the original listing for *A. marshallensis* that would indicate ecology, all specimens I have collected from Eniwetok, the type locality, came from under rocks on a sandy bottom in a somewhat protected cove on the lagoon side of one of the islets.

The specific name is derived from the Greek *rhothion*, meaning breakers or surf, and *nastes*, meaning inhabitant.

Athanas esakii Kubo

Athanas esakii Kubo, 1940*a*. J. Fish. Inst. Tokyo 34(1): 93–95, fig. 13*a–p*.

DISCUSSION: This small and obviously immature specimen was collected with numerous and larger specimens of *A. marshallensis* Chace apparently in a single ecological niche. On the basis of ecology, therefore, the separation of the two species is doubtful.

The specimen appears to be distinct from *A. marshallensis* only in the presence of an acute infracorneal tooth, all traces of which are lacking in *A. marshallensis*. While this characteristic does not appear to be reliable in other species of this genus, as in *A. areteformis*, the lack of intergrading specimens would make the placement of *A. marshallensis* in synonymy at this time a questionable step.

The chelae of this specimen are not exactly like either *A. marshallensis* nor *A. esakii*, but sufficiently close to both that the differences could easily be the result of immaturity. In this specimen the chelae have the following proportions:

	Merus	Carpus	Palm	Fingers
Smaller chela	1.5	1.0	1.0	0.6
Larger chela	1.3	0.8	1.0	0.5

Kubo reported that in his female specimen, somewhat larger than this, the chelae were noticeably asymmetrical; in this specimen the chelae were almost the same size.

DISTRIBUTION: Kubo's specimens came from Kusaie in the Caroline Islands while our specimen came from Eniwetok and was found under a boulder in the sand on the lagoon side of an islet.

Athanas verrucosus sp. nov.

Fig. 4

TYPE SPECIMEN: An ovigerous female, carapace length of 3.9 mm., total length of 11 mm., collected from coralline ridge, ocean (windward) reef, Parry Island, Eniwetok, 3 March 1957, by A. H. Banner (station BE-23). Sole specimen known.

DESCRIPTION: Body form usual. Rostrum short, reaching about to end of first antennular article; acute in dorsal view, triangular with straight sides; in lateral view with dorsal margin curved upward towards tip, ventral margin with double curve and bearing small tuft of setae; rostrum and carapace without carina. Supracorneal teeth distinct, acute, reaching almost to end of cornea; extracorneal teeth larger, exceeding length of cornea; infracorneal projection absent. Corneas covered posteriorly by collar between supra- and extracorneal teeth. Pterygostomial corner projecting but rounded.

Antennular peduncle short and heavy, with second article almost twice as long as broad. Superior distal margins of first and second articles each armed with four strong teeth. Stylocerite narrow, with tip reaching to near end of second article. Upper flagellum with only trace of bifurcation. Antennal peduncle also heavy. Basicerite thick, lateral region projecting as a broad tooth, bearing broadly acute tip. Carpocerite very heavy, only 1.5 times as long as broad, and 1.3 times broader than thick; tip reaching beyond end of antennular peduncle. Scaphocerite with tip of lateral spine reaching slightly beyond end of antennular peduncle, squamous portion broad and rounded, almost as long as lateral spine. Antennal flagellum reaching posteriorly to end of second abdominal segment.

Mouth parts protruding as those in *A. paragracilis* Coutière and *A. huikau* Banner with inflated labrum and with psalistome of mandibles expanded and almost hemispherical; teeth on psalistome small and numerous.

Chelipeds symmetrical except for 10 per cent difference in size. Ischium heavy, 0.7 length of merus, bearing five to six movable spines on inferior, three on superior margin. Merus compressed, triangular in section, with inferior surface flat and less broad than sides; outer face 1.5 times as long as broad at maximum breadth. Carpus 0.8 as long as merus, proximally very thin and narrow, distally greatly expanded to be 0.5 as broad as long; triangular in section; distal margins slightly projecting to cover base of chela. Chela short, 1.8 times length of merus, flattened, with thickness 0.5 of maximum breadth; inner face flattened, outer face convex; suboval area of outer face running from base to articulation of flattened dactylus; area distally delimited on inferior side by rounded shoulder; triangular area of lower distal margin of palm and proximal portion of finger armed by strongly projecting papillae, those best developed longer than broad at base and turned distally; setae arising between bases of papillae; inner face without papillae. Dactylus 0.4 as long as palm, curved, crossing tips with fixed finger, armed with two low rounded teeth fitting exactly with cutting edge of fixed finger.

Second legs markedly shorter than third legs, with length from meral-carpal articulation equal to combined lengths of ischium and merus. First and fifth carpal articles subequal; second, third, fourth articles subequal, each about 0.4 length of first or fifth article; first carpal article proximally narrow, about half width of fifth article.

Third legs robust. Ischium unarmed, 0.5 length of merus. Merus unarmed, 0.4 as broad as long. Carpus armed distally on superior margin with rounded tooth, on inferior margin with subterminal movable spine; almost 0.6 as long as merus, slightly more than half as broad as merus. Propodus at most slightly longer than merus, slightly curved, with five inferior and one distal spines; spines leaving middle portion of propodus unarmed. Dactylus curved, acute, simple, bearing tuft of setae. Fourth legs similar but with spines of propodus more continuous in arrangement. Fifth legs with only three inferior spines on propodus; "brush" feebly de-

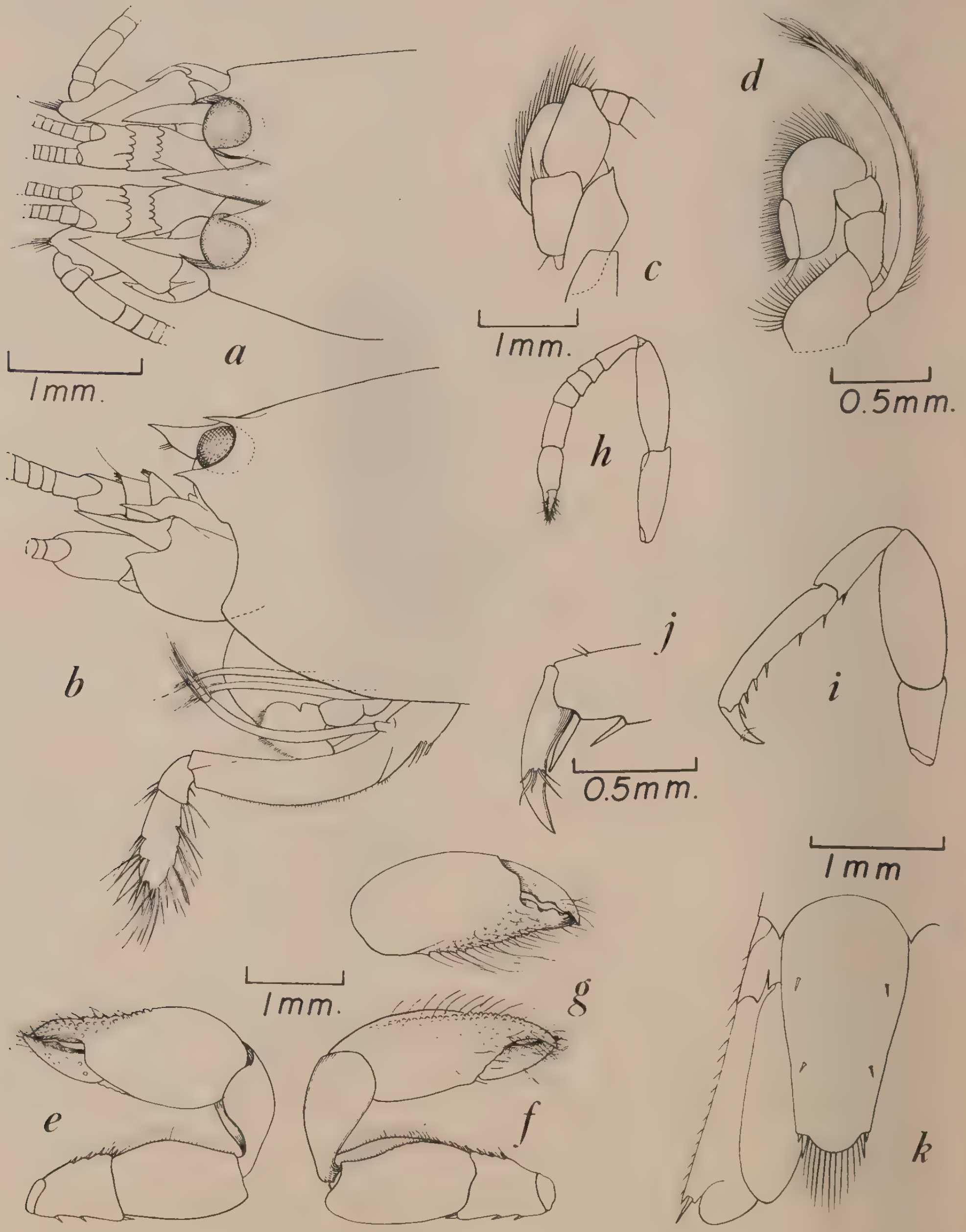
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FIG. 4. *Athanas verrucosus* Banner. *a, b,* Anterior body region; *c,* antennal peduncle, inferior aspect, in situ; *d,* second maxilliped; *e,* smaller cheliped, lateral view; *f,* smaller cheliped, medial view; *g,* smaller chela, outer face, viewed flat; *h,* second legs; *i, j,* third leg and dactylus; *k,* telson and uropods.

veloped, with only three rows of light setae found distally.

Abdomen normal except anterior pleura greatly expanded, posterior pleura small; pleura of sixth segment articulated. Telson normal, sides almost straight, tapering, 2.2 times as broad anteriorly as posteriorly, 4 times as long as broad posteriorly; tip extended and rounded. Uropods normal, narrow and long.

Branchial formula including five pleurobranchs, no arthrobranchs, and mastigobranchs extending back to second thoracic leg, setobranchs to third. No anal tubercles.

DISCUSSION: In the old genus *Athanas* this species is closely related to none; in the old genus *Arete*, now united with *Athanas*, this species is most closely related to *A. borradailei* (Coutière, 1903: 9) and *A. ghardaqensis* (Ramadan, 1936: 15). From both of these species it is separated by the five-jointed carpus and the presence of papillae on the palm. The difference in the chelae could be from growth or sexual dimorphism. A point for point comparison reveals other more minor differences. This species differs from *A. ghardaqensis* by a greater number of articulations in the base of the inner flagellum, by the presence of a small tooth on the basicerite, and by longer uropods. From *A. borradailei*, this species is distinguished by: 1. A more sinuate lower margin of the rostrum and a triangular shape (when seen in dorsal view); 2. the presence of serrations on the distal ends of the antennular articles; 3. the presence of many articulations in the antennular flagellum; 4. slight differences in the last article of the external maxilliped; 5. on the chelipeds, the presence of spines on the ischium, and slight differences in the proportions of the merus and carpus in addition to the presence of papillae on the palm; 6. a broader merus of the third legs, being less than 2.5 times as long as broad instead of three times. Also *A. borradailei* is reported to lack all thoracic epipodites, while this species has masigobranchs on the base of the chela and second legs. Neither Coutière nor Ramadan discussed the mouthparts.

Each of these three species were described on the basis of a single individual. While the differences listed above, especially in the carpus of the second legs, the chelae and the branchial formulae may be valid for their separation, the three specimens are so similar in general configuration and in the structure of the appendages and rostral front that their specific separation is very doubtful, particularly in view of the variation in other species of this genus. However, with only one specimen of each nominal species, it appears to be safest to leave them as separate species.

The name *verrucosus* refers to the "warty" condition of the palm of the large chela, a character in which this species appears to differ from both related species.

Athanas indicus (Coutière)

Arete dorsalis var. *indicus* Coutière, 1903. Bull. Soc. Philom. Paris IX, 5(2): 85.

Arete indicus Coutière, 1905*b*. Fauna and Geog. Maldive and Laccadive Archipelagoes 2(4): 863, figs. 134–135.

Arete iphianassa de Man, 1910*a*. Tijdschr. Ned. Dierk. Ver. II, 11(4): 312; 1911, Siboga Exped. 39a^1(2): 164, pls. 3, 4, fig. 11; 1922, Siboga Exped. 39a^4(5): 22, pl. 3, fig. 11.

——— Banner, 1956. Pacif. Sci. 10(3): 325.

Arete intermedius Yu, 1931. Bull. Mus. Hist. Nat., Paris II, 3(6): 513–514, fig. 1.

Arete kominatoensis Kubo, 1942. Dobutsugaku Zasshi [Zool. Mag., Tokyo] 54: 82–85, figs. 1, 2.

DISCUSSION: The habitat of 15 of 16 specimens from Aitutake was carefully observed while the collections were made. They came from the inner, but growing, portion of a windward reef, in a pool about six feet deep; every specimen was associated with the boring sea urchin, *Echinometra*, and were found both on the body of the urchin between the spines and within the smooth rounded cavity produced by the urchin. While most of the other specimens were not as carefully observed during their collection, the ones that were noted (as from Eniwetok) were so associated. Evidently, not all individual specimens of *Echinometra* have shrimp in association, for *Echinometra* was frequently encountered while collecting and the shrimp are quite uncommon in the collection.

For the following discussion of variation within the species, it was considered best to study a single population thereby ruling out differences that might be caused by ecological or geographic races. For this reason the 15 specimens from Aitutake were studied intensively and those from other archipelagoes were used merely as supplements to the study.

Four species closely related to *A. indicus* have been described: *A. iphianassa* de Man, *A. amboinensis* de Man, *A. intermedius* Yu, and *A. kominatoensis* Kubo (all save the last described under the genus *Arete*). Of these, only *A. amboinensis* appears to be distinct; it will be discussed under *A. dorsalis* in the following section.

de Man stated that his species *A. iphianassa* was similar to *A. indicus,* but could be distinguished by the characteristics compared in the accompanying tabulation.

In this series of specimens each of the criteria is either bridged or almost bridged:

1. The length of the extracorneal spines varies both in absolute length and in length relative to the eyes; both described conditions were found in this single series.

2. The basal portion of the outer antennular flagellum is found to vary from four to six articles, with most having four or five articles.

3. The carpocerite is found to vary in the length-breadth relationship from 1:1.5 to 1:2.7; some of this may be due to different rotation of the carpocerite itself.

4. The outer distal margin of the outer uropod may be either straight or curved outward near the tip; all of the males have straight margins, but not all of the females have curved margins.

5. Similar to the condition discussed in the next section for *A. dorsalis,* the females and the smaller males have straight cutting edges of their large and small chelae; however, the two intact large males have teeth developed, one with a single tooth on the fixed finger, none on the dactylus, the other with two teeth on the fixed finger and one on the dactylus.

6. The proportions of the carpal articles of the second legs are extremely variable, with the first article varying from 1.4 to 3.0 times as long as broad distally; in some, also, the first article is approximately equal in length to the sum of the following carpal articles, in others it is almost twice as long.

7. The spines on the propodus of the third legs vary in number from four to nine, and also in development, with some scarcely more than slight hairs, and others strong and well developed.

Also like *A. dorsalis* the development of the rostrum varies conspicuously. In one specimen the tip reaches beyond the end of the third antennular article, in four it reaches some distance along the third article, in eight it reached somewhere in the length of the second article (most to near the tip of the article) and in one it reaches only to the end of the first article.

The other specimens in the collections available, including those reported from Saipan as *Arete iphianassa* (Banner, 1956: 325), fall within the range of variation reported above with the exception of three fragmentary specimens from Canton Island. These three, unfortunately mostly without legs and with but two chelae among them, all have slightly different

A. iphianassa	*A. indicus*
1. Extracorneal spines equal in length to the eyes.	1. Extracorneal spines slightly longer than the eyes.
2. Four articles on basal portions of outer antennular flagellum.	2. Six articles in same.
3. Carpocerite 1.5 times as long as broad.	3. Carpocerite 3.0 times as long as broad.
4. Outer distal margin of outer uropod straight.	4. Outer distal margin of outer uropod curved outward.
5. Various minor proportions of the large chelae, but principally with that of the male bearing 2 teeth on the dactylus and one on fixed finger.	5. Fixed finger of large chela of male bearing 1 tooth, dactylus curved but unarmed.
6. Various proportions in second leg, but most conspicuous in the first article of the carpus which is 5 times as long as broad distally.	6. First carpal article 3 times as long as broad distally.
7. Propodus of third legs bearing 8 to 12 spines.	7. Propodus of third legs bearing two to three spines.

rostrums: while its tip reaches to near the end of the second antennular article, well within the range specified above, it was considerably broader and thicker. Possibly more important, however, is the fact that the stylocerite also reaches only to the end of the second antennular article, instead of to the end of the third, a condition found in no other specimens. It may well be that these represent a new species or geographic or ecological subspecies, but with only three specimens, all in very bad condition, it is impossible to decide with certainty.

The other two nominal species also fall well within the range of variation. *A. intermedius* was separated by Yu from *A. indicus* by a slightly longer rostrum, reaching to one-quarter of the length of the third antennular article, and by the presence of 12 spinules on the propodus of the third leg. As shown in the listing above, both of these characteristics are very variable, and the separation of *A. intermedius* seems without basis.

There is more doubt about the combination of *A. kominatoensis* with this species. Unfortunately Kubo did not contrast his species to *Arete,* where it belonged under the old classification (it has only four articles in the carpus of the second leg) but to *Athanas.* By contrasting the description and figures of Kubo with *A. indicus* the three differences are found: 1. The antennular peduncle is 2.2 times as long as broad instead of 3.0 (using the entire visible length of the peduncle divided by the breadth of the second article). 2. Kubo reports and shows a slight dorsal carina extending back to the middle of the carapace, while in *A. indicus* there is no true carina but rather a broad ridge terminating slightly behind the eyes. 3. The inferior margin of the merus of the third legs bears distally a slight tooth while in *A. indicus* it bears a strong tooth. It may be that these are valid criteria, especially the porportions of the antennular peduncle and dorsal carina—the development of the tooth on the third leg has been shown to be variable in the related *A. dorsalis*—and none of the specimens available closely approach the condition described by Kubo. However, in view of the wide variation already reported in this species and in *A. dorsalis* these seem to be questionable characteristics for a specific separation, yet it may be this form, being found as it is in the waters of southern Japan, is a separate subspecies.

DISTRIBUTION: This species has been reported from Djibouti, Maldives and Laccadives, Indonesia, China, and southern Japan. In the present collection we have specimens from Canton, Aitutake, Bora Bora, and the northern Marshall Islands. They were found in heads of dead coral and associated with the boring sea urchin *Echinometra.*

Athanas dorsalis (Stimpson)
Figs. 5, 6

Arete dorsalis Stimpson, 1861. Proc. Acad. Nat. Sci. Philad. 12: 32.

(?) *Athanas mascarinicus* Richters, 1880. Beitr. Meeresfauna der Insel Mauritius und der Seychellen, Decapoda, p. 164.

Arete dorsalis var. *pacificus* Coutière, 1903. Bull. Soc. Philom. Paris IX, 5(2): 87, figs. 31–34.

Arete maruteensis Coutière, 1905*a*. Bull. Mus. Hist. Nat., Paris 11(1): 19, figs. 1–6.

Arete maruteensis var. *salibabuensis* de Man, 1910*a*. Tijdschr. Ned. Dierk. Ver. II, 11(4): 313; 1911, Siboga Exped. 39a^1(2): 169, pl. 4, fig. 13.

DISCUSSION: To determine the validity of the separation of the three species and subspecies listed above, the specimens in the collection, especially a single collection of about 50 from Namu Island, Marshalls (Station 3167, J. E. P. Morrison), were examined closely. Of these specimens from a single locality, about 30 intact specimens were measured, and the findings confirmed by examination of the specimens from other parts of the Pacific.

Rostrum: In general the form of the rostrum is anteriorly a sharp triangle with an acute tip, while between the eyes the sides approach a parallel condition. In most the tip of the rostrum reaches to the end of the first antennular article or to the first half of the second article; in three specimens it reaches well into the second half of this article, and in one it reaches the beginning of the third article. In most cases it is between 1.6 to 2.1 times as long as broad.

Extracorneal Teeth: In most these are well developed, but to varying degree, and there is

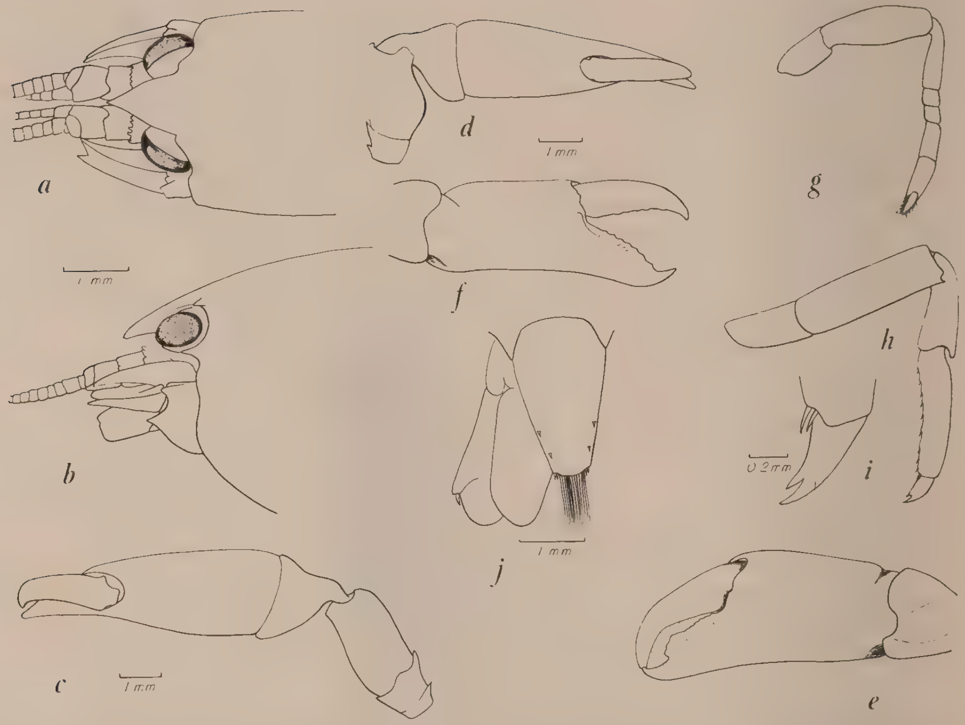

FIG. 5. *Athanas dorsalis* (Stimpson), a 5.5 mm. (carapace length) ovigerous female from Raroia, Tuamotus, Station 1847. *a, b,* Anterior region, dorsal and lateral aspects; *c, d,* large and small chelae, lateral view; *e, f,* same, from lower side; *g,* second leg; *h,* third leg; *i,* third leg, dactylus; *j,* telson and uropod.

a gradual series from those with pronounced teeth to the few with very slight teeth and to the one specimen (from the Tuamotus) without any teeth.

Antennular and Antennal Peduncles: Usually the stylocerite reaches to near the end of the antennular peduncle, the scaphocerite and carpocerite exceeding the stylocerite slightly; in no case are the differences in length pronounced, and at times the relationships change.

Large Chela: This appendage is found to exhibit strong growth and sexual differences (see Fig. 6*a–f*), with the young of both sexes showing a more or less uniform taper to the fingers which bear minute serrations on the basal two-thirds and the distal third being smoothly rounded to the curved tip. In adult females there is commonly an outgrowth of an irregular lobe proximal to the distal curve on the larger chela, while the other chela remains more like that found in the young. In some of the largest males the large chela has developed an exceedingly large tooth on the fixed finger, against which the dactylus closes; however, in other large males and in all smaller males this tooth is variously developed and much smaller. In both sexes the development of the chelae varies considerably between individuals of the same size, and in one very large ovigerous female the tooth of the fixed finger is as fully developed as that of the large male.

Small Chela: In most specimens, male and female, the cutting edge of the finger bears numerous low irregularities which stop abruptly in a tooth that may be obtuse or a right angle. The distal portion is curved. However, in some the irregularities are considerably smoothed, and the final tooth may be low and rounded.

Second Legs: In the merus the length-breadth ratio varies from 1:2.5 to 1:3.7, with most of the specimens bearing the ratio between 1:2.8 to 3.0. Only in a small series the relative lengths of the carpal articles and hand were measured, and these show that the extent of variation is similar to that of the merus.

Third Legs: Three characteristics of the third legs have been carefully observed: the length-breadth ratio of the merus varies from 1:2.5 to 1:3.4, with most of the specimens with the ratio between 1:2.9 to 3.1. The final outer tooth of the inferior margin in no specimen is large and no specimen is lacking, with the maximal development being about that shown in Figure 5*h*, while in the minimal development the tooth is barely visible, and is scarcely more than an obtuse irregularity; it also varies from slightly acute to obtuse. The length-breadth ratio of the propodus exhibits less variation than do the other measured articles, ranging from 1:4.0 to 1:4.6, with most of the specimens grouping around 1:4.5.

Telson: In all of the specimens except three the telson is found to be 3.2 to 4.0 times as long as the posterior margin is broad, with most 3.2 to 3.3 times. In two specimens the telson is only 3.0 times as long as broad, and in one it is 4.2 times as long.

The extent of this variation destroys the validity of the separation of *A. maruteensis* and *A. dorsalis.* Coutière separated his species (which he originally called *A. dorsalis pacificus*) upon the following characteristics: 1. shape of rostrum; 2. traces of extracorneal spines; 3. shape and armature of large and small chelae; 4. relative proportions of the carpal articles and chelae of second legs (for this character it should be noted that in the specimens measured some would be like *A. dorsalis* in two of the relative measurements and like *A. maruteensis* in the third); 5. the length-breadth relation of the articles of the third leg, and the presence of a definite tooth on the merus as opposed to being "coupè á angle droit" in *A. maruteensis.* To these differences de Man adds, in his separation of the subspecies *A. maruteensis salibabuensis* the proportions of the rostrum and merus of the second and third legs. In the group of specimens measured each of the characteristics was found to be

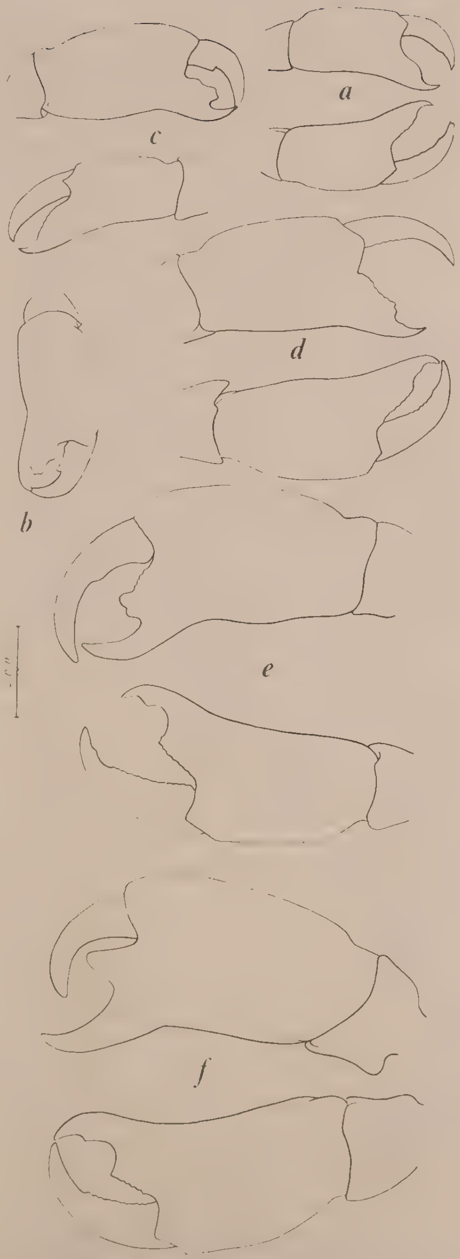

FIG. 6. *Athanas dorsalis* (Stimpson), variations in the development of the chelae. *a,* Male of 3.3 mm. carapace length; *b,* male of 3.5 mm. carapace length; *c,* male of 3.85 mm. carapace length; *d,* male of 4.95 mm. carapace length; *e,* male of 4.95 mm. carapace length; *f,* male of 5.2 mm. carapace length. All drawn to same scale.

variable, with the range of variation not only bridging the supposed differences between the nominal species and subspecies, but also extending beyond any previously reported condition. It is interesting to note that the specimens that agreed best with *A. dorsalis* were those from Raroia, not too far from the type locality of *A. maruteensis*, while the specimens from the Marshalls were more like the description of *A. maruteensis*.

The exact status of *A. mascarinicus* Richters is not known, as the description, without figures, is inadequate. It may be a synonym of this species; it may be the same as, and take priority over *A. indicus* or *A. amboinensis;* it may be regarded as a *nomen dubium;* or it may be a separate and valid species. Unless the type specimen can be redescribed, we feel it is safest to consider it as a synonym of *A. dorsalis*.

On many of these specimens, including the large group from the Marshalls, it was specified that they were collected from large sea urchins of the genus *Heterocentrotus;* however, for some their habitat was specified as "coral" (as was that of Stimpson's original specimen). Whether this indicates that the species normally lives only on sea urchins but may desert them if the urchin is disturbed, as by a collector, or whether it indicates that the species may live either on coral or sea urchins is not known. At least, no significant differences were found between those collected from urchins and those collected from unspecified "coral."

Athanas amboinensis (de Man, 1910*b*: 25–27, figs. 1–6) is, at least, closely related to *A. dorsalis*, more closely than *A. indicus* (Coutière); it may be found to be a synonym. However, as none of the specimens in the collection approach the proportions of the slender chela and narrow telson given by de Man as specific characteristics, there is no evidence that the two should be combined.

DISTRIBUTION: Stimpson's original specimens came from Hongkong and it has been reported from Djibouti, Indian Ocean, Indonesia, New Caledonia, Kermadec Islands and Samoa. In the present collection we have about 70 specimens, the majority from the Marshall Islands, 2 specimens from Canton Island, 1 from Fiji and 6 from the Tuamotus. At least 50 of the specimens were commensal with the sea urchin *Heterocentrotus*.

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Reprinted from PACIFIC SCIENCE, *vol. XIV, no. 2, April, 1960*

Fatal Shark Attack, Oahu, Hawaii, December 13, 1958[1]

ALBERT L. TESTER[2]

ON DECEMBER 13, 1958, a large shark believed to be *Galeocerdo cuvieri,* the tiger shark, was responsible for the death of 15-year-old William (Billy) Weaver in water about 12 feet in depth off Lanikai on the windward (east) coast of the island of Oahu, Hawaii. Although the story of the tragedy was well covered in the local newspapers, a condensed version has been prepared which includes information of interest to scientists who are concerned with factors motivating shark attack. In preparing the account which follows, conflicting stories have been resolved and additional information has been obtained by correspondence and interview with several of the persons directly or indirectly involved. Additional information on shark identification, shark fishing, etc., was supplied by the staffs of the Board of Agriculture and Forestry, Division of Fish and Game, and the Bureau of Commercial Fisheries, Pacific Oceanic Fisheries Investigation.

DESCRIPTION OF THE INCIDENT

A party of six boys including the victim (Billy Weaver) and five friends (Terry Oakland, age 14; Tom Replogle, 14; Garrett Goo, 13; Brook Collins, 10; and Charles Collins, 9) were swimming and surfing about noon off a reef near Twin Islands (Mokulua Island) about ¾ mile off Lanikai (Fig. 1). They had three surfboards which were light green, red and "natural" in color, three air mattresses which were red on one side and blue on the other, and an 8-foot sailboat, without mast or sail, which was white in color and anchored near the reef. The sky was clear but the water was rough with whitecaps and good-sized waves. The boys kept together; never was one more than 75–100 feet from the others.

About 1 p.m. Brook Collins was resting in the boat with his surfboard across it; Charles Collins was resting on his surfboard beside the boat, holding on to the anchor line—he was afraid of the waves after "pearl diving" on one. The four older boys were surfing off the reef. Garrett Goo and Terry Oakland, on air mattresses, and Tom Replogle, on the light green surfboard, caught a wave and rode a short distance. Billy Weaver, on an air mattress, failed to catch the wave. When about 50 yards away, the boys noticed that Weaver was clinging to the mat, apparently in difficulty. On hearing a feeble cry for help, Goo swam over, saw blood in the water, and realized that Weaver had lost a leg. The three boys attempted to support the victim and called to Brook Collins to bring the boat over. After some difficulty in freeing the anchor from the coral, Brook Collins hauled it up and started rowing. As the boat was coming too slowly, Garrett Goo swam to it, climbed aboard, and pushed the surfboard off the boat to make more room for rowing. Brook Collins, standing up in the boat, saw a large shark surface 30 feet away, and screamed "Shark." The two boys supporting the victim pushed him toward the reef, and swam frantically to the boat. By the time they reached the boat he had disappeared. As they could not approach the spot where he had been last seen without risk of swamping the boat in the waves, the boys rowed to shore and summoned help.

A Fire Department rescue squad arrived at 2:30 p.m. and sped to the scene in a borrowed 25-foot Chris-Craft boat. Local residents in other boats joined in the search. The body was finally

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[1] Contribution No. 125 of the Hawaii Marine Laboratory, University of Hawaii. Manuscript received April 6, 1959.

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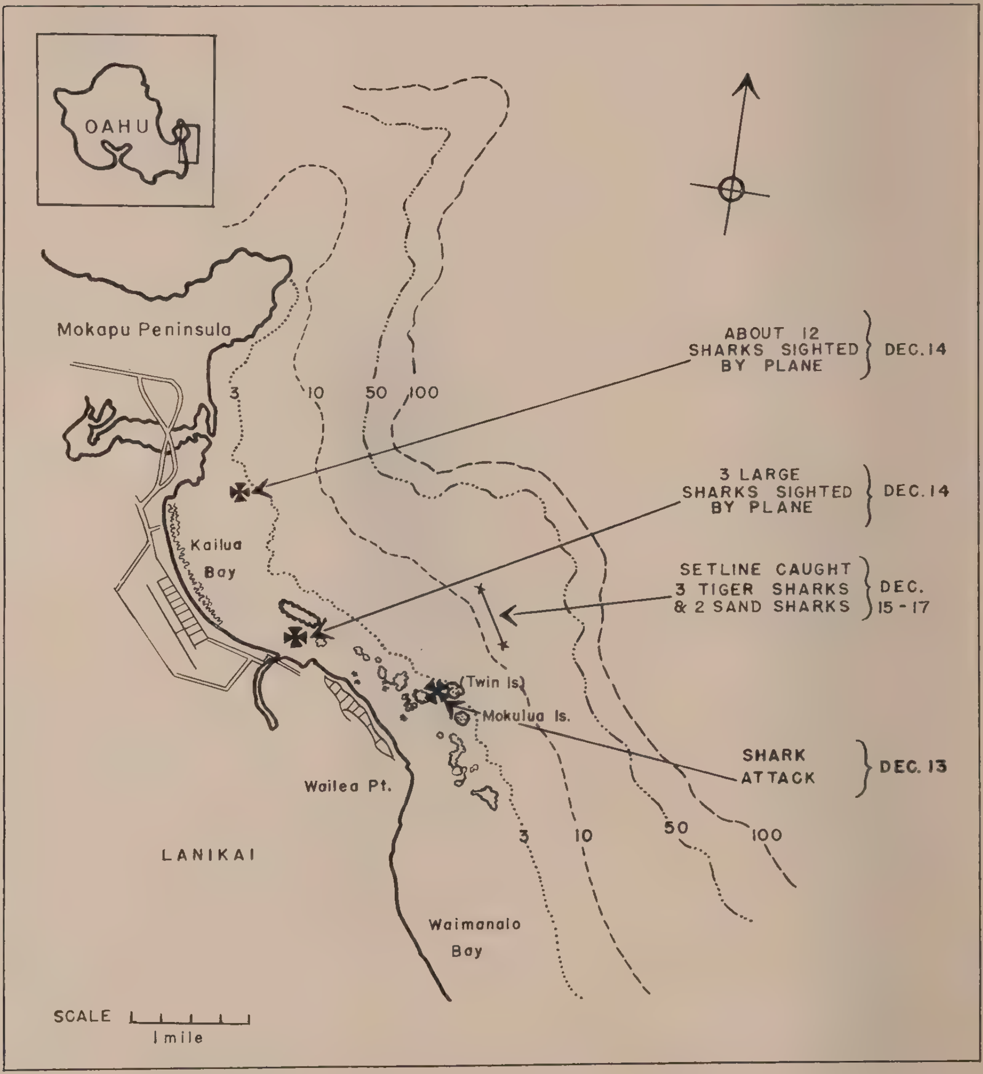
OAHU
Mokapu Peninsula
3
10
50
100
ABOUT 12 SHARKS SIGHTED BY PLANE
DEC. 14
3 LARGE SHARKS SIGHTED BY PLANE
DEC. 14
SETLINE CAUGHT 3 TIGER SHARKS & 2 SAND SHARKS
DEC. 15 - 17
Kailua Bay
(Twin Is)
Mokulua Is.
SHARK ATTACK
DEC. 13
Wailea Pt.
LANIKAI
3
10
50
100
Waimanalo Bay
SCALE
1 mile

FIG. 1. Coastline of Oahu, showing places where sharks were sighted.

located by a helicopter crew from Kaneohe Marine Air Station in a hole in the reef seven feet deep, and it was recovered by a local resident, John G. Ferreira, by skin diving. The shark, variously estimated at 15 to 25 feet in length, was still cruising nearby, its dorsal fin about 1½ feet out of the water. Attempts to revive the boy with artificial respiration both on board the boat and on shore were unsuccessful. A deputy coroner stated the shark bite had stripped away the flesh six inches above the knee and completely removed the right leg from the knee joint. The victim died from loss of blood, drowning, shock, or a combination of all three.

ATTEMPTS TO CATCH THE SHARK

On December 14, 1958, attempts were made by employees of the Division of Fish and Game and by local residents to capture the shark. The Fish and Game employees set an 8-hook shark setline in the shallow water off the reef where the incident had taken place but without success. In the meantime, Piper Cub pilots searching the area spotted two schools of sharks in the adjacent waters of Kailua Bay (Fig. 1). One group of three large sharks was reported cruising just off Flat Island, 200 yards offshore from the public beach. The second school of about a dozen sharks was spotted on the north end of the bay. Local residents converged on both areas hoping to kill the sharks with high-powered rifles but were unsuccessful.

From December 15 through December 17, 1958, under the personal direction of C. Eric Reppun, President, Board of Agriculture and Forestry, and Michio Takata, Director, Division of Fish and Game, the Division's research vessel "Makua" fished a 24-hook setline (flagline or buoyed longline) offshore from the reef in about 70–80 feet of water (Fig. 1). The catch consisted of three tiger sharks and two sand sharks. Two of the tiger sharks were 12 feet in length and weighed 750–800 pounds; the third was 11 feet in length and weighed 410 pounds. The two sand sharks *(Eulamia menisorrah?)* were eight to nine feet in length and weighed about 350 pounds.

IDENTITY OF THE SHARKS

It seems most likely that the fatal attack was by a large tiger shark (*Galeocerdo cuvieri*). One of the searchers described the shark (to Herbert Mann, Bureau of Commercial Fisheries) as having blotches on its sides and a blunt nose, thus eliminating most other local species including the great white shark (*Carcharodon carcharias*). Moreover, in the recent six months of shark fishing to assess local abundance, the Division's ship "Makua" has caught only two species by setline in inshore water (50–120 feet in depth)—34 tiger sharks and 33 sand sharks. The largest tiger shark taken during this period, 14½ feet in length and 1,200 pounds in weight, approaches the reputed size of the Lanikai killer. However, an element of uncertainty is introduced by Brook Collins' observation that the dorsal fin of the shark appeared black along the edge, suggesting some species other than the tiger.

COMMENT ON SHARK ATTACK

It is noteworthy that the fatal attack occurred before the swimmers were aware that a shark was in the vicinity. If the boys had been skin diving, rather than surfing, they may have discovered its presence. If the shark surfaced prior to the attack, its dorsal fin must have passed unnoticed in the rough surface water.

It is noteworthy that three of the four boys exposed to attack were using air mattresses. Manipulation of the mattress in pushing, boarding, and paddling, requires much more activity than does a surfboard. It is possible that the shark was attracted to the area by this unusual commotion. The vicitm is likely to have been threshing his arms and legs extensively while attempting to catch the wave which carried away his companions.

Tom Replogle reported that he had seen coconut floats, such as are used to mark fish traps, near the scene of the tragedy. A turtle was also observed nearby. It is possible that the shark was attracted to the area by fish caught in the traps or by the turtle.

Although there is no on-the-spot record of water temperature, it was probably about 23° C. This temperature was recorded at the time of the tragedy for the salt water system at the Hawaii Marine Laboratory, Kaneohe Bay, some five miles distant. The water is pumped continuously from a depth of about 10 feet.

SHARK ABUNDANCE

Although quantitative data are not available over a sufficient period of time to measure changes in shark abundance, observations by fishermen and skin divers indicate the abundance has increased in the last few years. This has been attributed to several possible causes:

(1) Cessation of shark fishing because of a recent law (Hawaii Food, Drug and Cosmetic Act, 1941) requiring the labelling of ingredients in Japanese-style fish cake. Although most of the sharks used for this purpose were taken incidental to tuna longlining, which is still active, it is possible that the fishermen now cut the leader line when a shark is captured, allowing

it to go free. This practice would speed up the handling of the gear when using the recently introduced automatic hauler.

(2) Reduction in the inshore fish population, inducing sharks to frequent shallow waters and to become bolder in their search for food. There is not much doubt that the reef fish population is at a low level of abundance because of both commercial and sport fishing pressure. The latter must have increased greatly with the introduction of SCUBA diving gear.

(3) Increase in shark population for some unknown reason. Possibly an increase in abundance occurred following the war period of reduced effort in the longline fishery.

There appears to have been an increase in shark attacks during the past 10 years as compared with a previous 60-year period. Of the 5 (perhaps 6) known fatalities since 1886, 3 (including the present) have occurred in the last 10 years. Of the 11 incidents involving injury by sharks since 1886, 5 have occurred in the last 10 years. Whether the increase is due to the increased number of swimmers and consequent increased number of exposures is unknown.

PUBLIC REACTION

There was immediate and widespread concern over the shark incident, together with public demand for action to reduce the hazard. Bounties were offered by a private individual (Bill Wills, $20 each for 10 sharks) and by a radio station (KPOA, $100 per shark over 15 feet, $25 per smaller shark for sharks caught until the end of December in the vicinity of the tragedy). An action program for reducing shark abundance on a continuing basis was proposed by the Board of Agriculture and Forestry and endorsed by several windward Oahu associations on December 18, 1958. Its activation is contingent on funds to be raised by public subscription. The plans call for a one-vessel, scientifically directed shark fishing program embracing all inshore waters of Oahu. Should this become a reality, efforts will be made to not only control the local shark population but at the same time to gain information on the species composition, abundance, distribution, life history, and behavior of the sharks.

The Billy Weaver Shark Control Program was started April 1, 1959, using the vessel "Holokahana I" with Fred J. Inouye as master. Using three units of 24-hook long-line gear, 595 sharks were caught from the inshore waters of Oahu during the remainder of the year. Of these, 71 were tiger sharks.

Hallucinatory Mullet Poisoning

A Preliminary Report *

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Introduction

A number of fish from tropical and temperate seas have been reported to cause from mild to lethal cases of poisoning among persons eating them. Most of the toxins implicated appear to be of non-bacterial origin. Types of fish poisoning have been separated into broad classes both according to the fish eaten and to the symptoms produced (Halstead 1956, 1959). A type of intoxication differing from those previously reported has appeared in Hawaii over the years, caused primarily by the eating of certain mullet (Mugilidae) and surmullet or goatfish (Mullidae) from restricted localities on two islands, Kauai and Molokai. The poisoning is always mild and non-fatal.

In the course of our studies we have not been able to reproduce the disease in the laboratory nor have we observed the human symptoms first hand, but we have interviewed enough individuals who have been stricken with the disease to be able to establish the syndrome. The reason for this initial report, then, is to define the intoxication as a reaction separate from other types of fish intoxication so that others may recognize it and supply additional clinical details.

Symptomatology

This type of intoxication, for which we propose the name "Hallucinatory mullet poisoning"† appears to involve primarily the higher nervous system and produces symptoms in the patient, if awake, of dizziness, loss of equilibrium, lack of co-ordination, hallucinations and mental depression; if symptoms begin while the patient sleeps, he develops nightmares, giving rise to the common names of one of the causative fish: "nightmare *weke*" or "crazy surmullet". Other symptoms vary, with some victims reporting an itching or burning of the throat immediately after eating, others a muscular weakness and even a partial paralysis of the legs. Gastrointestinal upset, nausea, or diarrhoea are rarely reported in these cases. The onset of symptoms has been reported to be from ten minutes to two hours after ingestion; symptoms usually persist for a few hours, but occasionally have been reported to last up to twenty-four hours. A few cases have been treated by local physicians (unreported in the literature) and all the victims independently interrogated by the authors were in general agreement in their description of the syndrome.

From the many types of fish poisoning described, the syndrome of this type of poisoning appears to be clearly distinguished at least by the following characteristics: (1) the early onset and short duration of the symptoms; (2) the presence of hallucinations and extreme mental depression; (3) the general lack of gastrointestinal disorder. Other symptoms, which may or may not occur, such as sensory involvement, lack of co-ordination and muscular weakness of the legs are also found in *Ciguatera* and other types of intoxication. It is worthy to note that the species involved in this type of intoxication from Hawaii have also been implicated in the *Ciguatera* poisoning from other areas (Belotte, 1955; Halstead, 1956, 1959; Halstead and Bunker, 1954a, 1954b; Ross, 1947). This may be due to the confusion of symptoms, especially those related by the non-English speaking indigenes of the islands, or it may indicate that the same species of fish may be toxic in two different ways in different areas.

Aetiology

In Hawaii four species of fish, representing two families, have been reported to have caused the illness. All are popular food fishes in Hawaii. Two species of mullet (Mugilidae) are most commonly implicated, *Mugil cephalus* L., and *Neomyxus chaptalli* (Eydoux and Souleyet). The other family is that of the goatfish or surmullet (Mullidae), which also contains two toxic species: *Mulloidichthys samoensis* (Gunther) and *Upeneus arge* (Jordan and Evermann)

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* Contribution No. 126 of the Hawaii Marine Laboratory.

†This name could be rendered into a Greek or Latin descriptive term with a combination such as "ichthyosarcephialtilepsis", but we prefer to retain the English in the hope that it will be more easily pronounced and understood, albeit less in the medical tradition.

the last being referred to locally as "nightmare *weke*". In addition, several people have reported that the surgeonfish or tang, *Acanthurus sandvicensis* (Streets) and the rudder fish, *Kyphosus cinerascens* Forskal., have also caused the symptoms described, but no first-hand accounts of this poisoning were found.

In the Hawaiian Archipelago the fish are reported to be toxic from only two islands: Kauai, primarily in the Anini area, but extending from Pilaa to Haena; and Molokai, in the Pilaau region. In these areas the fish are considered to be toxic only in the months of June, July and August. On the island of Molokai the fishermen report that the toxic fish cannot be distinguished from the non-toxic fish; on Kauai, on the other hand, they report that the toxic mullet and goatfish often have red telangiectatic blotches on the surface of the lips and on the sides of the head.

This fish toxicity was first reported by Jordan, Evermann and Tanaka in 1927, when they gave an account of 30 to 40 Japanese labourers who suffered "delirium" and were "mentally paralyzed" after eating "*weke pahala*" *(Upeneus arge)* from the island of Molokai. They stated that "It is agreed that the poison lies in the brain". They sent a fresh specimen of the species to Dr. Nils Larsen of The Queen's Hospital in Honolulu, who fed the brain to a cat which "at once went crazy, but recovered, as in fact, all cases soon recovered." They also reported that Dr. Larsen fed cats the flesh of *U. arge* as well as other species and the brain of this goatfish captured in the winter, all without effect. Later records of the poisoning from the Hawaiian Islands (Tinker, 1944; Nichols and Bartsch, 1945; Titcomb and Pukui, 1952; Fish and Cobb, 1954; Randall, 1958) are all apparently based on this basic report by Jordan *et al.* (1927).

To our knowledge, the only other reports in the scientific literature of this type of reaction were those of van Pel (1959) from Norfolk Island and J. L. B. Smith from South Africa. Van Pel reported intoxication from a fish known locally as the "dream fish", possibly *Kyphosus vaigiensis* (Quoy and Gaimard). The author relates (personal correspondence) that he questioned about twenty people who had consumed the flesh of the "dream fish", and they declared "they had terrible nightmares as soon as they went to sleep". J. L. B. Smith (1953) stated about members of the family Mullidae: "It is best, however, not to eat the heads as the brains are said to cause convulsions." It should be also noted that Dr. Bruce Halstead of the World Life Research Institute was quoted in a press release (Associated Press story from Colton, California, by Ralph Dighton, dated 19th September 1959) as finding a hallucinogenic substance in fish; he was quoted as stating he could not disclose the species nor the locality where it was captured "because Russia is exceedingly interested in nerve drugs such as this".

From interrogation of the people living near the afflicted areas on the two islands, there appeared to be a wide range of individual tolerance to the intoxication. In one family three members were mildly affected and the fourth unaffected from the fish in a common meal; in another case, a man and his wife were strongly affected, his sister mildly so but the sister's husband did not develop any symptoms from eating the same lot of fish. Similarly, there are those who refuse to touch the implicated fish from the known toxic areas, having been poisoned once or several times by them, while others in the same community stated that they commonly eat the indicted species of fish with impunity all the year round. The reaction is not likely to be psychosomatically induced as it has been reported to have occurred in very young children who were fed the fish "and woke up screaming and trying to crawl out of their cribs" (report from a personal interview on Molokai). Neither can the reactions be ascribed to an individual allergy to fish of these species for all those reporting cases remarked that they commonly eat these fish from "safe" areas or "safe" seasons. Some of those affected reported, as did Jordan *et al.* (1927), that the toxic portion of the fish was the head, and that the body could be eaten safely; others reported developing hallucinations or nightmares from eating only the flesh of the body. All agreed that it made no difference whether the fish be eaten raw, boiled, steamed or fried. Some of the persons interviewed reported that their cases were so severe as to compel them to visit physicians for relief.

Experimental Investigations

After interviewing many individuals to obtain their first-hand accounts of their symptoms, it was attempted to induce the intoxication in the laboratory. Eight specimens of *Mugil cephalus* and two of *Mulloidichthys samoensis* from Anini on Kauai, captured during July, each specimen showing the red, telangiectatic blotches, were eaten by members of the investigation without ill-effect; because of the reported higher toxicity of the viscera and brain, these parts of each fish were also eaten. There was no reaction. Further, 53 specimens of *M. cephalus* between 128 and 374 millimetres fork length, and 12 specimens of *Upeneus arge*, between 222 and 286 millimetres fork length, were fed to cats and mongooses. Cats were chosen because of the success of Dr. Larsen's previous test (Jordan, *et al., loc. cit.);* mongooses were used because of their success for preliminary assay for toxins of the *Ciguatera* type (Banner and Boroughs, 1958). The fish were captured in the toxic areas of Kauai and Molokai during July and August of 1959, quick-frozen and transported to the laboratory in a frozen condition. The flesh, viscera, brains, and heads without the brains, were fed separately to animals in amounts equivalent to between 5 per cent and 15 per cent of the bodyweight of the test animal. Twenty-three individual feedings were made on mongooses and 15 on cats. No unusual actions were observed in the test animals following these feeding tests. The animals remained in a quiescent state, normal for well-fed animals and if mild intoxication produced hallucinations and mental depression, these were not detectable.

These tests indicate that either the toxic fish are not as common as was indicated by many of the individuals living near the affected districts on Kauai and Molokai, or that it may not be possible to detect the toxicity with the test animals used.

Discussion

Without controlled laboratory experiments carried on in conjunction with field observations of the biology of the fish, it is impossible to offer a plausible explanation of this seasonal and regional toxicity found in these restricted species. However, several of the possible causes should be considered.

It is most unlikely to be caused by bacterial action upon the dead fish, as in putrescence, for all persons interviewed indicated that the fish that caused the poisoning were reasonably fresh, and usually eaten almost immediately after capture. One victim, a fisherman from the island of Molokai, stated that he caught the fish while he was tending the net; he cleaned and boiled it immediately, and had eaten the fish less than a half hour after it was swimming in the water; his symptoms were so severe that he visited the local physician.

The local fishermen attribute toxicity to items in the fish's diet. Some fishermen merely report it is differences in the " ground " where the fish feed which causes a marked change of diet. To determine if there was a difference in the diet, an examination of the stomach contents of three species was made. The contents of the stomachs of *M. cephalus* captured in July, 1959 from the toxic areas on Kauai and Molokai revealed that the fish had been feeding on diatoms and other unicellular algae in about the same proportions as reported by Hiatt (1944) for this species from the fish ponds of Hawaii. This is also in agreement with reports on the food of this species from other parts of the world (Hiatt and Strasburg, in press; summary in Thomson, 1954). The stomach contents of *M. samoensis* from the " toxic " areas revealed that they were subsisting upon crabs, shrimps and amphipods; the stomachs of *U. arge* contained portunid crabs, shrimp, and pleuronectid fishes. These findings, too, are in general agreement with reports for these species from other areas.

Most common is the statement that the fish become toxic because of *limu* (Hawaiian for alga) (Anon, 1957). If pressed, many fishermen blame the bluegreen alga, *Lyngbya majuscula* Gomont, that is abundant during the summer months in the toxic areas. Similarly, a number of marine biologists have attributed other fish toxins, especially those of the *Ciguatera* type, to blue green algae, specially *Lyngbya* (Dawson *et al.*, 1955; Randall, 1959; Dawson, 1959). However, the relationship is conjectural, and no strong evidence has been adduced that any type of fish toxicity is attributable to this or any other alga. In Hawaii it is true that *Lyngbya majuscula* is abundant in the toxic areas, and that some strains of the alga will cause dermatitis when applied to the skin in humans, and death when eaten by laboratory animals (Banner, 1959; Chu, 1959); it has also been known to be toxic to higher animals (Tilden, 1937). However, *Lyngbya majuscula* is abundant on many Hawaiian beaches — for example, it is often cast up in windrows on the beaches of Kaneohe Bay, on Oahu—and the toxic fish come only from very restricted areas which do not include most areas where *Lyngbya* is abundant. Moreover, some of the areas that have produced the most toxic strains of alga, as Laie on Oahu, have never been reported to have had fish poisoning. Finally, none of the species of fish known to be toxic commonly eat *Lyngbya: Mugil* feeds on diatoms, and no alga recognizable as *Lyngbya* was found in its stomach, while *Mulloidichthys* and *Upeneus* are carnivores, feeding mostly upon crustacea; if the crustacea had been the transmitters of the toxin (as suggested by Vinberg (1954) for crawfish in Russian lakes), then other fishes feeding on these crustaceans would be expected to carry the same toxins.

Acknowledgements

These studies were carried on in conjunction with studies on the biology and chemistry of the *Ciguatera* type of toxins (A.E.C. Contract AT (04-3)-235), with special supplementary funds granted by the Honolulu Chamber of Commerce. The authors are indebted to Mr. George Akau, Bureau of Pure Food and Drugs, Department of Health, Hawaii, for information on this condition, and to Mr. Robert Morris who aided in the field work.

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Reprinted from the JOURNAL OF TROPICAL MEDICINE AND HYGIENE, *April, 1960*

Reprinted from The Journal of Parasitology, October, 1960,
Vol. 46, No. 5, pages 648–650.

HAWAIIAN HELMINTHS. IV. *PARACARDICOLA HAWAIENSIS* N. GEN., N. SP. (TREMATODA: SANGUINICOLIDAE) FROM THE BALLOON FISH, *TETRAODON HISPIDUS* L.*

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The fish blood flukes described here were collected from the mesenteric veins of *Tetraodon hispidus* at the Hawaii Marine Laboratory, University of Hawaii. The fish were collected by trapping in Kaneohe Bay, Oahu. All of the 10 fish examined for blood flukes were found to harbor the eggs or the eggs and *Paracardicola hawaiensis*. The presence of eggs was determined by examining a small piece of host liver flattened between 2 microscope slides. Hundreds of eggs were found in most of the 10 hosts.

The worms, secured by flushing out mesenteric veins, were fixed in cold Heidenhain's solution and stained with celestine blue B. They were mounted in H.S.R. Microscopic Mounting Medium.

All measurements are in millimeters.

Paracardicola n. gen.

Generic diagnosis: Sanguinicolidae. Body small, slender, laterally spined along most of length. Oral sucker rudimentary. Esophagus long, about one-third of body length, slender, slightly sinuous. Intestine H-shaped, posterior ceca considerably longer than anterior. Gonads in posterior half of body, anterior testis immediately in front of ovary, posterior testis behind posterior extent of uterus. Seminal vesicle elongate and saccular. Ovary compact. Uterus postovarian, relatively long, with few loops. Small vitelline glands extend from mid-esophageal level to ovary. Eggs with terminal spine. Genital pores separate but close together, near mid-seminal vesicle level. Parasitic in circulatory system of marine fish.

Genotype: P. hawaiensis in *Tetraodon hispidus* L.

Paracardicola hawaiensis n. sp.

Species diagnosis: Description based on 10 specimens. With characters of genus. Body elongate, slender, laterally spined, 0.72 to 1.92, av. 1.26 in length and 0.04 to 0.11, av. 0.079 in maximum width. Body with lateral, comb-like spines along most of length. Oral sucker terminal, weakly developed, approximately 0.016 in diameter. Esophagus tubular, elongate, 0.24 to 0.57, av. 0.46 in length and 0.006 to 0.012, av. 0.011 in maximum width. Intestine H-shaped, anterior ceca shorter than posterior. Anterior ceca of approximately the same length, 0.037 to 0.118, av. 0.068 long and 0.015 to 0.025, av. 0.021 in maximum width. One posterior cecum longer than the other, the shorter cecum 0.09 to 0.48, av. 0.29 and the longer 0.11 to 0.53, av. 0.32 in length. Maximum widths of posterior ceca similar, 0.015 to 0.025, av. 0.021. Anterior testis immediately in front of ovary, 0.075 to 0.3, av. 0.17 in length and 0.03 to 0.081, av. 0.06 in maximum width. Posterior testis behind uterus, not as well developed as anterior testis, 0.087 to 0.23, av. 0.16 in length and 0.028 to 0.06, av. 0.04 in maximum width. Ducts from testes enter anterior end of seminal vesicle. Seminal vesicle elongate, saccular, weakly convoluted, sperm-filled, 0.12 to 0.15, av. 0.137 in length and approximately 0.025 in maximum width. The seminal vesicle bends anteriad for a short distance to terminate as the male genital pore. Although the wall of the terminal portion of the male duct is slightly thickened, there is no distinct cirrus. The

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Received for publication December 14, 1959.

* These studies were aided by a contract between the Office of Naval Research, Department of the Navy, and the University of Southern California, NR 165-252. The opinions and assertions contained herein are the private ones of the author and are not to be construed as official or reflecting the views of the Navy Department or the naval service at large.

Contribution No. 127, Hawaii Marine Laboratory, University of Hawaii, Honolulu.

compact ovary is immediately posterior to the anterior testis. The oviduct is joined by the vitelline duct a short distance posterior to the ovary. The small vitelline glands extend posteriorly from the mid-esophageal level to the posterior margin of the ovary. They are lateral to and between the intestinal ceca. The uterus extends posterior to the seminal vesicle, then loops anteriad to a level near the ovary, then bends posteriorly to open at the female genital pore. The distal portion of the uterus is expanded and has thickened walls. It probably is here that the egg shell is formed. There is a raised group of cells surrounding the female pore. Eggs about 0.08 long and 0.037 wide with terminal spine approximately 0.009 long. These eggs were recovered from the host's liver and contained a ciliated miracidium lacking eyespots. A tubular excretory bladder opens at the posterior end of the body.

Type specimen: Paracardicola hawaiensis, deposited as number *5716* in the Hancock Parasitology Collection.

Host: Tetraodon hispidus L., balloon fish, in mesenteric veins.

Locality: Kaneohe Bay, Oahu, Hawaii.

DISCUSSION

Paracardicola most closely resembles the genus *Cardicola* which Short (1953) erected with *Psettarium cardiocolum* Manter, 1947, as type and to which he assigned *C. laruei.* Short changed the spelling of *cardiocolum* to *cardicola.* The correct spelling of Manter's species is *Cardicola cardiocolus* following the Copenhagen Decisions on Zoological Nomenclature (1953) which states, "names consisting of words ending with the Latin term—'cola' are to be treated as masculine, unless the name is taken from a word given in the standard Latin dictionary as being of common gender and the author of the name stated in the original description that the name was feminine in gender." *Paracardicola* differs from *Cardicola* and all other genera of fish blood flukes in having 2 testes. *Cardicola* and *Selachohemecus* Short, 1954, have 1 testis and the other genera have multiple testes (see Short, 1954). In *Paracardicola* the posterior intestinal ceca reach the anterior portion of the preovarian testis while in *Cardicola* they reach the ovary. There are additional differences in the gonoducts.

As in *Cardicola cardiocolus* (Manter, 1947), the uterine eggs appear to be without shells. The shell may be laid down in the lower end of the uterus and the egg laid soon afterward. Eggs of *Paracardicola hawaiensis* are very numerous in the liver of *Tetraodon hispidus* and must do considerable damage to this organ.

Manter (1947) and Short (1953) placed their new species of fish blood flukes in the family Aporocotylidae, but Yamaguti (1958) places both of these species in the Sanguinicolidae reserving Aporocotylidae for a single genus, *Aporocotyle.*

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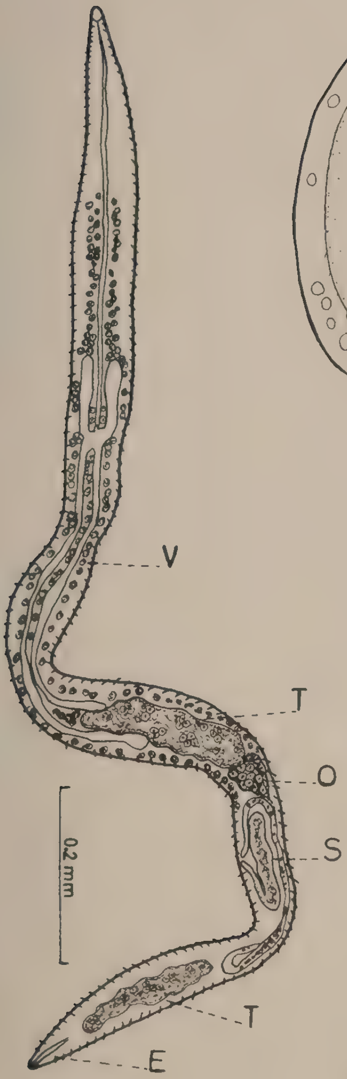
EXPLANATION OF PLATE I

FIGURES 1–6. *Paracardicola hawaiensis:* 1, Entire worm; 2, shelled egg containing miracidium and globules; 3, ovary and main portions of genital ducts; 4, egg immediately after release from ovary; 5, anterior end of worm showing rudimentary sucker; 6, comb-like spine from side of body; E, excretory bladder; O, ovary; S, seminal vesicle; U, uterus; V, vitellaria; VD, vitelline duct.

PLATE I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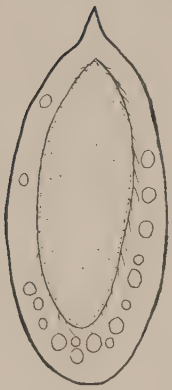

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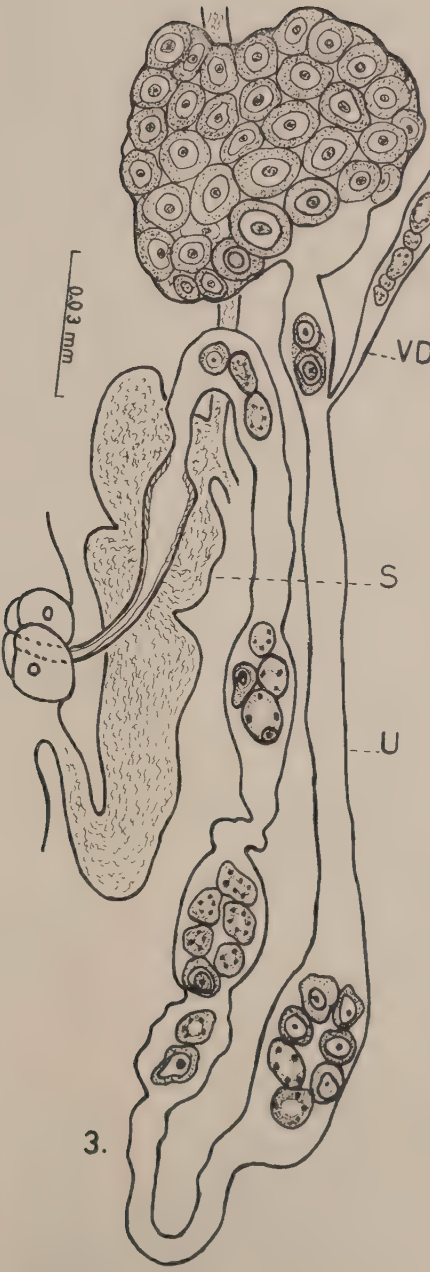

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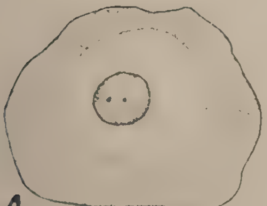

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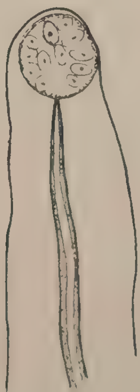

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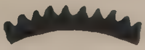

6.

Ecological Relationships of the Fish Fauna on Coral Reefs of the Marshall Islands

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[Reprinted from Ecological Monographs, **30**: 65-127. January, 1960]

ECOLOGICAL RELATIONSHIPS OF THE FISH FAUNA ON CORAL REEFS OF THE MARSHALL ISLANDS[1]

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INTRODUCTION

The greatly increased attention paid to scientific aspects of the central Pacific by American scientists following the close of World War II brought sharply into focus our exceedingly meager knowledge of this region. Problems faced by administrators of the newly created Trust Territory of the Pacific, and by those responsible for maximum safety during and after atomic weapons testing operations stimulated many studies of this vast portion of the globe, of which the study reported here was a part. Significant marine problems such as the nature and distribution of the poisonous fishes of the tropical Pacific islands, the effect of nuclear explosions and radioactive con-

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[1] Contribution No. 128, Hawaii Marine Laboratory, University of Hawaii.

tamination from weapons testing, and the possibility of commercial sources of marine food products required a thorough knowledge of the nature, extent, and community relationships of the marine fauna and flora. More significant, perhaps, in the long run will be the opportunity for learning more about the optima for utilizing sunlight and raw materials in this relatively isolated, but complex, ecosystem which apparently fluctuates in composition very little, if at all, from year to year, and has over a long period of time acquired a biota successfully adjusted competitively in the relatively constant environment of the tropical west-central Pacific Ocean. It has already been realized by Odum & Odum (1955) that important information might be secured on the relationship between organic productivity, energetic efficiency, and the standing crop structure of such coral reef communities. Moreover, the answers as to how steady state equilibria, such as the reef ecosystem, are self adjusted may be more easily revealed by more critical, comprehensive examination.

To reach reasonable interpretations of the energetics of production and utilization it is necessary, among other things, to determine the relationship between the standing crop, defined as the biomass of existing organisms per unit area, and productivity, defined as the rate of manufacture of this biomass per unit area (Odum 1953). Odum & Pinkerton (1955) indicate that, on a theoretical basis, systems of many types when in open steady state tend to adjust to maximum output of energy consistent with available input energy and a correspondingly low but optimum efficiency. Therefore, if the apparently steady state coral reef ecosystems tend to be similarly self adjusted regarding efficiency of energy utilization between trophic levels, and if the biota remains rather constant in composition as it certainly seems to do, then the pyramids of biomass should be roughly proportional to the standing crop for a particular coral reef area. It becomes paramount in importance, therefore, not only to know the taxonomic composition of the biota of reef areas under intensive study, but to have a rather clear concept of the biotic interaction of the species present to categorize them in proper trophic levels, and to know the community relationships in the various physiographic environments characteristic of the coral reef biotope. The importance of the type of information embodied in this paper may best be illustrated by the following statement made by Odum & Odum (1955), "Although the trophic relationships of most of the higher organisms on the reef are very imperfectly known, an attempt has nevertheless been made to make rough groupings by trophic level as to herbivores, carnivores, and decomposers."

PREVIOUS RESEARCH

Although numerous workers have reported on the feeding habits of Pacific fishes, only two authors report in any comprehensive manner and neither makes any attempt to express his results as meaningful ecological aspects. In a very painstaking study of the digestive system and feeding habits of fishes of Japan, Suyehiro (1942) provided far more information on these subjects than had theretofore been available. Moreover, he included an extensive review of the literature which now makes it unnecessary to discuss this matter for the period preceding his publication. Suyehiro based his study on 88 families, 132 genera, and 150 species, providing a firm basis for many of the central Pacific families and genera. Only a few species reported by Suyehiro reach the central Pacific area. Al=Hussaini (1947) reported on a similar study of some 60 species in the vicinity of the Marine Biological Station at Ghardaqa, Red Sea, and included many of the widespread Indo-Pacific types. Randall (1955) reported on the fishes of the Gilbert Islands and included notes on food habits for a few of the specimens collected. Only two papers dealing with the Indo-Pacific fish fauna (Hiatt 1947a, 1947b), and these dealing with a special type of ecosystem, have approached the problem of food and feeding habits of fishes from the point of view of biotic interaction. Scattered accounts of feeding habits of Pacific fishes occur incidentally in other papers, and these will be mentioned in the species accounts where pertinent.

SCOPE OF THE PRESENT STUDY

Reported herein are accounts of the food and feeding habits and ecological relationships of 56 families of Marshallese fishes, covering 127 genera and 233 species. Some idea of the completeness of coverage of the study may be gained from the fact that in the Marshall Islands there are about 225 genera and about 600 species of fish. We have examined therefore somewhat more than half of the genera and slightly less than half of the species known to be present. Because the Marshallese fauna is part of the widespread Indo-Pacific faunal complex, the significance and applicability of this study extends a great deal further than the west-central Pacific Ocean islands.

The study was initiated at Bikini Atoll in the summer of 1947, as part of the Bikini Scientific Resurvey to determine what changes had resulted, if any, from Operations Crossroads, continued at Arno Atoll during the summer of 1950 as part of the Coral Atoll Project of the Pacific Science Board, and completed at Eniwetok Atoll during the summer of 1955 as part of the regular studies being carried out at the U. S. Atomic Energy Commission's Eniwetok Marine Biological Laboratory. The total number of individual fish stomachs examined was 2,051, of which 209 were examined at Bikini, 1,185 at Arno, and 657 at Eniwetok.

A systematic list of the families, genera, and species covered by this food study follows, and a few species, not examined for food, are cited elsewhere in the text.

- Family Carcharhinidae (gray sharks)
    - *Carcharhinus melanopterus* (Quoy and Gaimard)
    - *C. menisorrah* (Müller and Henle)
- Family Triakidae (smooth dogfishes)
    - *Triaenodon obesus* (Rüppell)
- Family Orectolobidae (carpet sharks)
    - *Ginglymostoma ferrugineum* (Lesson)
- Family Mobulidae (manta rays)
    - *Manta alfredi* (Krefft)
- Family Dussumieridae (round herrings)
    - *Spratelloides delicatulus* (Bennett)
- Family Clupeidae (sardines)
    - *Harengula kunzei* Bleeker
- Family Ophichthidae (snake eels)
    - *Leiuranus semicinctus* (Lay and Bennett)
    - *Brachysomophis sauropsis* Schultz
- Family Muraenidae (moray eels)
    - *Echidna zebra* (Shaw)
    - *E. leucotaenia* Schultz
    - *E. polyzona* (Richardson)
    - *Uropterygius xanthopterus* Bleeker
    - *Rabula marshallensis* Schultz
    - *Gymnothorax pictus* (Ahl)
    - *G. petelli* (Bleeker)
    - *G. javanicus* (Bleeker)
    - *G. flavimarginatus* (Rüppell)
    - *G. buroensis* (Bleeker)
    - *G. undulatus* (Lacepede)
    - *G. margaritophorus* Bleeker
    - *G. ruvelli* (McClelland)
    - *G. fimbriatus* (Bennett)
    - *G.* sp.
- Family Congridae (conger eels)
    - *Conger noordzieki* Bleeker
- Family Moringuidae (whip eels)
    - *Moringua macrochir* Bleeker
- Family Synodontidae (lizard fishes)
    - *Synodus variegatus* (Lacepede)
    - *Saurida gracilis* (Quoy and Gaimard)
- Family Belonidae (needle fishes)
    - *Strongylura gigantea* (Temminck and Schlegel)
    - *S. incisa* (Cuvier and Valenciennes)
- Family Hemiramphidae (halfbeaks)
    - *Hyporhamphus laticeps* (Günther)
    - *H. affinis* (Günther)
- Family Bothidae (flounders)
    - *Bothus mancus* (Broussonet)
- Family Holocentridae (squirrel fishes)
    - *Myripristis berndti* Jordan and Evermann
    - *M. microphthalmus* Bleeker
    - *M.* sp.
    - *Holocentrus sammara* (Forskål)
    - *H. lacteoguttatus* Cuvier and Valenciennes
    - *H. microstomus* Günther
    - *H. laevis* Günther
    - *H. diadema* Lacepede
    - *H. spinifer* (Forskål)
    - *H.* sp.
- Family Syngnathidae (pipe fishes)
    - *Corythoichthys flavofasciatus conspicillatus* (Jenyns)
    - *C. intestinalis waitei* (Jordan and Seale)
- Family Aulostomidae (trumpet fishes)
    - *Aulostomus chinensis* (Linnaeus)
- Family Fistulariidae (cornet fishes)
    - *Fistularia petimba* Lacepede
- Family Atherinidae (silversides)
    - *Stenatherina temmincki* (Bleeker)
    - *Allanetta ovalaua* (Herre)
    - *Pranesus pinguis* (Lacepede)
- Family Mugilidae (mullets)
    - *Neomyxus chaptali* (Eydoux and Souleyet)
    - *Crenimugil crenilabis* (Forskål)
- Family Sphyraenidae (barracudas)
    - *Sphyraena qenie* Klünzinger
- Family Polynemidae (threadfins)
    - *Polydactylus sexfilis* (Cuvier and Valenciennes)
- Family Scombridae (tunas)
    - *Gymnosarda nuda* (Günther)
    - *Euthynnus affinis yaito* Kishinouye
    - *Katsuwonus pelamis* (Linnaeus)
- Family Carangidae (jacks)
    - *Trachurops crumenophthalmus* (Bloch)
    - *Trachinotus bailloni* (Lacepede)
    - *Carangoides ferdau jordani* Nichols
    - *Caranx melampygus* Cuvier and Valenciennes
    - *C. lessoni* Bleeker
    - *Elagatis bipinnulatus* (Quoy and Gaimard)
- Family Apogonidae (cardinal fishes)
    - *Apogon novemfasciatus* Cuvier and Valenciennes
    - *A. snyderi* Jordan and Evermann
    - *A. exostigma* (Jordan and Starks)
    - *A. nigrofasciatus* Lachner
    - *A. novaeguineae* Cuvier and Valenciennes
    - *A. erythrinus* Snyder
    - *Apogon* sp.
    - *Gymnapogon philippinus* (Herre)
    - *Paramia quinquelineata* Cuvier and Valenciennes)
    - *Cheilodipterus macrodon* (Lacepede)
- Family Priacanthidae (bigeyes)
    - *Priacanthus cruentatus* (Lacepede)
- Family Serranidae (groupers)
    - *Epinephelus merra* Bloch
    - *E. fuscoguttatus* (Forskål)
    - *E. kohleri* Schultz
    - *E. hexagonatus* (Bloch and Schneider)
    - *E. macrospilos* (Bleeker)
    - *E. spilotus* Schultz
    - *Variola louti* (Forskål)
    - *Cephalopholis urodelus* (Bloch and Schneider)
    - *C. miniatus* (Forskål)
    - *C. argus* Bloch and Schneider
    - *Anyperodon leucogrammicus* (Cuvier and Valenciennes)
    - *Plectropomus truncatus* Fowler
- Family Pseudochromidae
    - *Plesiops melas* Bleeker
    - *P. nigricans* (Rüppell)
    - *Pseudogramma polyacantha* (Bleeker)
    - *Pseudochromis tapeinosoma* Bleeker
- Family Pempheridae (sweepers)
    - *Pempheris oualensis* Cuvier and Valenciennes
- Family Lutjanidae (snappers)
    - *Lutjanus monostigmus* (Cuvier and Valenciennes)
    - *L. bohar* (Forskål)
    - *L. vitta* (Quoy and Gaimard)
    - *L. vaigiensis* (Quoy and Gaimard)
    - *L. gibbus* (Forskål)
    - *Scolopsis cancellatus* (Cuvier and Valenciennes)
    - *Gymnocranius griseus* (Schlegel)
    - *Lethrinus microdon* Cuvier and Valenciennes
    - *Aprion virescens* Cuvier and Valenciennes
    - *Gnathodentex aureolineatus* (Lacepede)
- Family Leiognathidae (Silver perch)
    - *Gerres argyreus* (Bloch and Schneider)
- Family Sparidae (snappers)
    - *Monotaxis grandoculis* (Forskål)
- Family Mullidae (goat fishes)
    - *Mulloidichthys samoensis* (Günther)
    - *Parupeneus trifasciatus* (Lacepede)
    - *P. barberinus* (Lacepede)
    - *P. cyclostomus* (Lacepede)
    - *Upeneus arge* Jordan and Evermann
- Family Cirrhitidae (hawkfishes)
    - *Amblycirrhitus arcatus* (Cuvier and Valenciennes)
    - *Paracirrhites forsteri* (Bloch)
    - *Cirrhitichthys aprinus* (Cuvier and Valenciennes)
    - *Cirrhitus pinnulatus* (Bloch)
- Family Siganidae (rabbit fishes)
    - *Siganus rostratus* (Cuvier and Valenciennes)
- Family Kyphosidae (pilot fishes)
    - *Kyphosus cinerascens* (Forskal)
- Family Chaetodontidae (butterfly fishes)
    - *Chaetodon lunula* (Lacepede)
    - *C. citrinellus* Cuvier and Valenciennes
    - *C. ephippium* Cuvier and Valenciennes
    - *C. vagabundus* Linnaeus
    - *C. reticulatus* Cuvier and Valenciennes
    - *C. auriga* Forskål
    - *Megaprotodon strigangulus* (Gmelin)
    - *Centropyge flavissimus* (Cuvier and Valenciennes)
- Family Acanthuridae (surgeon fishes)
    - *Acanthurus mata* Cuvier and Valenciennes
    - *A. xanthopterus* Cuvier and Valenciennes
    - *A. gahhm* (Forskål)
    - *A. olivaceus* Schneider
    - *A. triostegus triostegus* (Linnaeus)
    - *A. achilles* Shaw
    - *A. aliala* Lesson
    - *A. nigroris* Cuvier and Valenciennes
    - *A. guttatus* Bloch
    - *A. lineatus* (Linnaeus)
    - *Ctenochaetus striatus* (Quoy and Gaimard)
    - *Naso lituratus* (Schneider)
    - *N. unicornis* (Forskål)
    - *Zebrasoma veliferum* (Bloch)
- Family Scorpaenidae (scorpion fishes)
    - *Scorpaenodes parvipinnis* (Garrett)
    - *Scorpaenodes* sp.
    - *Scorpaenopsis gibbosa* (Bloch)
    - *Pterois radiata* Cuvier and Valenciennes
    - *P. volitans* (Linnaeus)
    - *Synanceja verrucosa* Bloch
- Family Caracanthidae
    - *Caracanthus unipinnus* (Gray)
- Family Platycephalidae (flatheads)
    - *Thysanophrys* sp.
- Family Pomacentridae (damsel fishes)
    - *Abudefduf sordidus* (Forskål)
    - *A. septemfasciatus* (Cuvier and Valenciennes)
    - *A. leucopomus* (Lesson)
    - *A. saxatilis* (Linnaeus)
    - *A. dicki* (Lienard)
    - *A. biocellatus* (Quoy and Gaimard)
    - *A. amabilis* (DeVis)
    - *A. glaucus* (Cuvier and Valenciennes)
    - *A. lacrymatus* (Quoy and Gaimard)
    - *Chromis atripectoralis* Welander and Schultz
    - *C. caeruleus* (Cuvier and Valenciennes)
    - *Dascyllus aruanus* (Linnaeus)
    - *Pomacentrus pavo* (Bloch)
    - *P. nigricans* (Lacepede)
    - *P. jenkinsi* Jordan and Evermann
    - *P. albofasciatus* Schlegel and Müller
    - *P. vaiuli* Jordan and Seale
- Family Labridae (wrasses)
    - *Epibulus insidiator* (Pallas)
    - *Gomphosus varius* Lacepede
    - *Pseudocheilinus hexataenia* (Bleeker)
    - *Labroides dimidiatus* (Cuvier and Valenciennes)
    - *Novaculichthys taeniourus* (Lacepede)
    - *Stethojulis axillaris* (Quoy and Gaimard)
    - *Stethojulis* sp.
    - *Halichoeres hoeveni* (Bleeker)
    - *H. marginatus* Rüppell
    - *H. hortulanus* (Lacepede)

- *H. trimaculatus* (Quoy and Gaimard)
- *H. margaritaceus* (Cuvier and Valenciennes)
- *Macropharyngodon meleagris* (Cuvier and Valenciennes)
- *M. pardalis* (Kner)
- *Thalassoma umbrostygma* (Rüppell)
- *T. quinquevittata* (Lay and Bennett)
- *T. lucasanum marnae* Schultz
- *T. hardwickei* (Bennett)
- *T. lutescens* (Lay and Bennett)
- *Cheilinus oxycephalus* Bleeker
- *C. chlorourus* (Bloch)
- *C. trilobatus* Lacepede
- *Coris angulata* Lacepede
- *C. gaimardi* (Quoy and Gaimard)
- *Hemigymnus melapterus* (Bloch)

- Family Scaridae (parrot fishes)
  - *Cryptotomus spinidens* (Quoy and Gaimard)
  - *Scarus bicolor* Rüppell
  - *S. sordidus* Forskål
  - *S.* sp.
  - *S.* sp.
  - *S.* sp.
  - *S.* sp.
  - *S.* sp.
  - *S.* sp.
  - *S.* sp.
- Family Gobiidae (gobies)
  - *Gnatholepis anjerensis* (Bleeker)
  - *Gobius ornatus* Rüppell
  - *Bathygobius fuscus fuscus* (Rüppell)
  - *Gobiodon erythrospilus* Bleeker
  - *G. rivulatus* (Rüppell)
  - *Paragobiodon echinocephalus* (Rüppell)
- Family Eleotridae (sleepers)
  - *Valenciennea violifera* Jordan and Seale
  - *V. strigata* (Broussonet)
- Family Microdesmidae
  - *Paragobioides grandoculis* Kendall and Goldsborough
- Family Echeneidae
  - *Echeneis naucrates* Linnaeus
- Family Parapercidae (sand perch)
  - *Parapercis cephalopunctatus* (Seale)
  - *P. clathrata* Ogilby
- Family Blenniidae (blennies)
  - *Aspidontus taeniatus* Quoy and Gaimard
  - *Istiblennius coronatus* (Günther)
  - *I. paulus* (Bryan and Herre)
  - *Exallias brevis* (Kner)
  - *Cirripectus variolosus* (Cuvier and Valenciennes)
  - *C. sebae* (Cuvier and Valenciennes)
- Family Brotulidae
  - *Dinematichthys iluocoeteoides* Bleeker
- Family Balistidae (trigger fishes)
  - *Rhinecanthus rectangulus* (Bloch)
  - *R. aculeatus* (Linnaeus)
  - *Balistapus undulatus* (Mungo Park)
  - *Balistoides viridescens* (Bloch and Schneider)
  - *Pseudobalistes flavimarginatus* (Rüppell)
  - *P. fuscus* (Bloch)
  - *Melichthys vidua* (Solander)
- Family Monacanthidae (file fishes)
  - *Amanses carolae* (Jordan and McGregor)
  - *Oxymonacanthus longirostris* (Bloch)
  - *Monacanthus* sp.
- Family Ostracionidae (trunk fishes)
  - *Ostracion cubicus* Linnaeus
- Family Tetraodontidae puffers)
  - *Arothron mappa* (Lesson)
  - *A. hispidus* (Linnaeus)
  - *A. meleagris* (Lacepede)
  - *A. nigropunctatus* (Bloch)
  - *Arothron* sp.
- Family Canthigasteridae (sharp-backed puffers)
  - *Canthigaster solandri* (Richardson)
- Family Diodontidae (spiny puffers)
  - *Diodon hystrix* Linnaeus

During the course of this study the authors were supported by several agencies all of which generously provided both funds, supplies, equipment, transportation, and shelter. The United States Atomic Energy Commission supported the studies at Bikini and at Eniwetok, the latter studies being carried out under the auspices of the A.E.C. Division of Biology and Medicine at the Eniwetok Marine Biological Laboratory. The study at Arno Atoll was part of the Coral Atoll Program sponsored by the Pacific Science Board of the U. S. National Research Council, under its major project Scientific Investigations in Micronesia. Funds to support the Coral Atoll Project were provided by the U. S. Office of Naval Research. Special acknowledgment is due to the Military Air Transport Service and to officials of the Civil Administrative Staff of the Trust Territory (Navy) for logistical support of this work.

The University of Hawaii through its Pacific Islands Research Fund provided generously for all the equipment and supplies for the work at Arno Atoll, and provided technical assistance in working up the mass of data collected for this study. Marian Adachi Kohn, staff artist for the Hawaii Marine Laboratory, drew the figures depicting habitat associations on the Marshallese coral reefs.

DESCRIPTION OF THE STUDY AREAS

The Marshall Islands are a group of atolls lying north of the Gilbert Islands and east of the Caroline Islands. All are enclosed in an area bounded by the parallels of latitude 4°30′N and 15°N and the meridians of longitude 161°E and 174°E (Fig. 1). They are about 2,500 statute miles west-southwest of Honolulu, Hawaii, and 4,700 statute miles from San Francisco. Most of the atolls are distributed along two chains which are nearly parallel and trend northwestward. The eastern is named the Ratak Chain (which includes Arno Atoll near its southern end) and the western the Ralik Chain (which includes Bikini at its northern end). Besides the two main chains there are several isolated outlying atolls, of which Eniwetok Atoll is one, lying west of the chain. Bikini Atoll is located between the parallels of latitude 11°30′ to 11°40′N and between the meridians of longitude 165°10′ and 165°40′E. Eniwetok Atoll is located between the parallels of latitude 11°20′ to 11°40′N and between the meridians of longitude 162° to 162°30′E. Arno Atoll is located between the parallels of latitude 7° to 7°30′N and between the meridians of longitude 171°30′ to 172°E. The physiographic features of Bikini Atoll and Eniwetok Atoll are set forth in great detail by Emery, Tracey, & Ladd (1954), and these features for Arno Atoll were described by Wells (1951).

The major ocean current systems in the Marshall Islands area are the westerly-flowing North and South Equatorial Currents and the easterly-flowing Equatorial Countercurrent lying between them. Most of the Marshall Islands lie athwart the North Equatorial Current which extends north of latitude 6°-8°N and occupies the zone of the northeast trade winds. The Equatorial Countercurrent lies south of the North Equatorial Current and usually has its southern boundary just north of the equator. Thus Arno Atoll is located in the divergence of these current systems which brings about upwelling and resultant high organic productivity. These hydrographic conditions, coupled with a higher rainfall and resultant terrestrial productivity, make the reefs of Arno Atoll more productive than those of Bikini and Eniwetok Atolls lying farther to the north.

Water temperatures at the surface in the Marshall Islands are among the highest found anywhere in the open ocean far from large land masses. During summer average temperatures range between 82° and 85°F. The average annual range of temperature along the entire island chain down to a depth of about 300 feet is only 3° to 4°F.

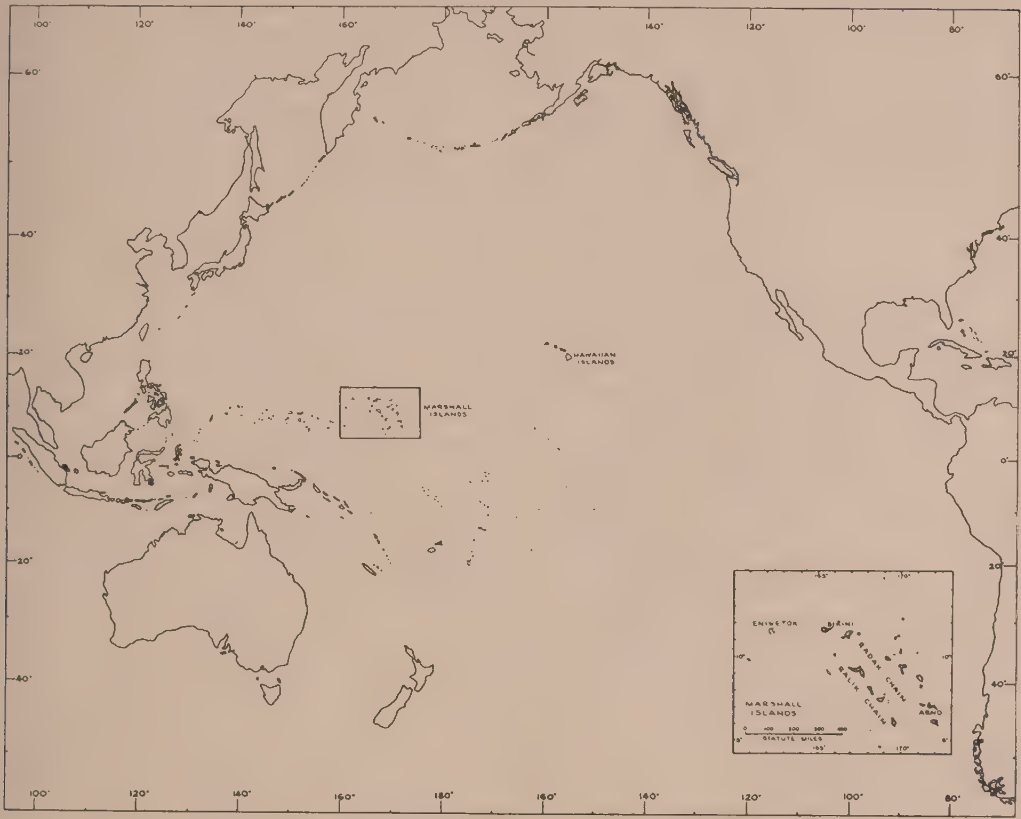

FIG. 1. The Pacific Ocean showing the location of Arno, Bikini, and Eniwetok Atolls.

Rainfall along the island chains varies considerably from north to south. At Arno the average rainfall is about 200 in, whereas at Bikini and Eniwetok it is about 50 in. The difference in rainfall is reflected in the surface oceanic salinity values which range from about 33.7 $^{0}/_{00}$ in the southern Marshall Islands to about 35.3 $^{0}/_{00}$ in the northern area of the chains. Although no data have been collected regarding tidal cycle effects on the salinity values across the reefs of Bikini and Eniwetok Atolls, such data from Arno Atoll indicate that a gradient occurs during low tides across the seaward reefs from about 50% oceanic salinity near shore to 100% oceanic salinity just off the seaward reef front. This phenomenon, associated with the runoff of fresh water from the Ghyben-Herzberg lens under the island, has a profound effect on the distribution of corals, and indirectly, if not directly, the distribution of fish on these seaward reefs (Hiatt 1958).

The tidal amplitude varies somewhat from the northern islands in the chains to those of the southern end. At Arno Atoll the mean tidal range is 3.8 ft and the mean spring tide range is about 4.1 ft. At Eniwetok and Bikini Atolls the mean tidal range is about 2.7 ft, while the mean spring tide range is about 3.9 ft. This tidal range is sufficiently extensive to change almost completely the biotic composition of the fish fauna on the flat, table-like seaward reefs which are virtually uncovered during low tides, but which are covered by about 2-4 ft of water during high tides.

Rather detailed descriptions of the reefs of Bikini and Eniwetok Atolls are given by Tracey, Ladd & Hoffmeister (1948), Ladd, Tracey, Wells, & Emery (1950), and Emery, Tracey, & Ladd (1954). Wells (1951) has described those of Arno. Consequently, only a brief summary will be presented here. The reefs of the Marshall Islands, like those elsewhere, are highly complicated structures which can be only roughly classified into three primary types, windward, leeward, and lagoon reefs. Most of these reefs exhibit well-developed zonation, the zones tending to parallel the reef front. The nature and extent of these zones depends on many factors, e.g., prevailing winds and currents, fresh water runoff from islands, and ecological factors determining the suitability of the environment for particular species. Although no two atoll reefs are identical, the major features which are controlled by wind, waves, and temperatures, have much in common.

The windward reefs, exposed to the prevailing trades that blow from the east and northeast during most of the year, differ markedly from the leeward reefs. The reef surface is comparatively flat and is covered with adequate water for most fishes only during periods of high tides. The outer marginal zones are usually flourishing and most often are bordered by a coralline ridge which receives the main impact of the waves. These reefs flats may be up to a half-mile in width, with several distinctive shoreward zones in which characteristic faunal and floral associations appear.

The leeward reefs are narrow, being only 200-500 ft in width. Their seaward margins are usually made irregular by surge channels which frequently extend inward 10-30 yds. No coralline ridge is present, and corals grow in great profusion, covering half or more of the reef surface. Usually, the leeward reefs are less elevated than those of the windward type so that the biota is resident. Only the largest of the roving carnivores slip over the reef front at high tide to forage on the reef flat.

Lagoon reefs vary depending upon their exposure to the prevailing wind. In protected areas there is a discontinuous series of irregular reef patches which extend from near shore to the outer slope leading to the deeper parts of the lagoon. These reef patches are not subjected to heavy wave impact, the only water movement aside from prevailing currents which affects them is the slow ocean swells which enter the lagoons through passages. Usually these conditions favor a luxuriant growth of coral in its more delicate form, imparting to these coral patches striking beauty. The fauna and flora are largely unaffected by tides and remain closely associated with the coral patches. Extensive sand and rubble flats separate the coral patches, and characteristic animal communities there contrast with those ecologically more closely tied to coral patches. On the leeward side of these atolls the lagoon reefs are better developed and frequently are continuous, because they receive fairly strong waves engendered by the prevailing winds which have a fetch of up to 20 miles or more across the lagoon. In some instances, these reefs come to resemble those characteristic of the windward side of the atoll, in that they frequently have an elevated algal ridge bordering the reef margin and may be flattened shoreward of the reef margin. However, they usually lack the distinct zonation characteristic of the seaward reefs of the windward side.

METHODS

Most of the fishes collected for this study were taken by poisoning sections of the reefs with rotenone. However, many were taken with spears, hook and line, explosives, and other techniques suitable for the occasion. The advantage of rotenone is that it almost simultaneously kills all fish in an area, and causes those deep in interstices of the corals and rocks, as well as those in burrows to come to the surface. In this way all members of a fish community can be collected and analyzed for their interrelationships as all niches filled give up their fish fauna for study.

The following data were recorded for each specimen examined: (1) standard length, (2) sex, (3) extent of development of the gonads, (4) nature of the alimentary tract, i.e., length, thickness of intestinal wall, presence or absence of a gizzard, (5) nature of the dentition and gill rakers, position and special features of the mouth, and (6) type of food items contained in the stomach, or, if empty, those found in the intestine.

For the food habits analysis the particular food items were listed and the numbers of fish containing the items were tallied. This method was used because it gives essentially the predilection of each fish species for particular items of diet. In studies of food and feeding interrelationships these types of data are most important. Such methods of analysis as the comparative quantities of different food items ingested become significant only when sufficient specimens are analyzed to ensure that one or a few large items taken by only one or a few fish do not give spurious percentages for the total. In most cases in the present study neither time nor specimens were available to add biomass or volume measurements. However, in those instances when a fish had consumed a great preponderance of a particular item, along with numerous other incidental items, it was noted in our records. For many species sufficient specimens were examined so that the percentage of fish containing the item became significant, and these are so listed in the systematic analysis of the food and feeding habits. If too few fish were available the results were recorded simply as the number of fish containing the item.

Naturally, collecting fish by means of rotenone poisoning resulted in many of the large carnivorous and predaceous species consuming smaller species which had succumbed earlier to the poison. Fish found in the stomachs which appeared too freshly caught were therefore discarded.

It will be obvious to the reader that biotic interrelationships and community groupings based solely on circumstantial evidence presented by food items in stomachs and structural features adapted for food getting, while exceedingly important, could not provide all the evidence needed to interpret data such as are presented in this paper. Consequently, it will be reassuring to state that hundreds of hours of underwater observations using skin-diving equipment have contributed very substantially to our results and interpretations. As a matter of fact, the analyses of natural aggregations in the various habitats on the reefs, to be presented later in this paper, were only possible by combining our field observations with the stomach analyses.

The results of our studies will be presented first by a systematic analysis and discussion of the food and feeding habits of the species, genera, and families represented. Following these data an analysis will be made of the major feeding habits characteristic of the species studied. Discussions will include such natural groupings as algal feeders, plankton feeders, omnivores, detritus feeders and scavengers, coral polyp feeders, and large roving carnivores. The interrelationships of naturally occurring assemblages on the reefs will be discussed also. In this section accounts will cover fish associated with mid-water and surface fauna, fish associated with the bottom, fish associated with rock and coral ledges and caverns, fish associated with branching corals and their dead bases, fish associated with solid coral heads, fish associated with the surf zone, fish associated with the windward sea reef flats, and fish associated with tide pools.

Discussions of the trophic levels represented by the fish studied will be presented also. Following this section the study will be summarized by a consideration of the results in the form of the food chains and the food web found on these coral reefs of the Marshall Islands.

FOOD AND FEEDING HABITS BY TAXONOMIC CATEGORIES

Family Carcharhinidae

Species: *Carcharhinus melanopterus* (black-tipped shark)
Number examined: Eniwetok, 3 specimens: 2 empty
Sex: 1 male; 1 female
Standard length: 690-1,200 mm

Two specimens were caught near the garbage dump; one stomach was empty and one contained garbage only. One specimen taken on the seaward reef flats had a partly digested fish in its stomach. This is the most common shark on the seaward reefs both on the windward and leeward sides of the atolls. It moves onto the reef flat as the tide rises, and forages widely. It also occurs on the lagoon reefs, but there the individuals are usually of larger size and are less numerous than on the seaward reefs. This shark seems to have a rather curious nature and many encounters with it in the water indicate that it has poor vision. Consequently, it usually approaches very closely to persons wading or swimming before it suddenly darts away. It habitually enters recently poisoned areas to devour small fish rendered moribund by rotenone, and is itself rather resistant to this poison. It is classed as a roving carnivore and scavenger.

Species: *C. menisorrah* (gray shark)
Number examined: Eniwetok, 1 specimen
Sex: Female
Standard length: 1,450 mm

One specimen was caught at the garbage dump, but the stomach was empty. This species is more common in the lagoons than is *C. melanopterus*, and is also found along the outer edge of the seaward reef front cruising in water 15-20 ft in depth. It frequently enters surge channels along the seaward reef. On numerous occasions this species has competed with us in picking up fish during poison station operations. At such times, individuals up to 7-8 ft in length enter water only 2-3 ft deep. It is classed as a roving carnivore and scavenger.

Family Summary

Members of the Family Carcharhinidae are by far the most abundant sharks on Marshallese reefs, and certainly occupy an important position among the carnivores as well as the scavengers of the coral reef community.

Family Triakidae

Species: *Triaenodon obesus* (white-tipped shark)
Number examined: Eniwetok, 1 specimen
Sex: Female
Standard length: 1,150 mm

One specimen caught near the garbage dump had no food in its stomach. Next to *C. melanopterus* this shark is the most abundant on Marshallese reefs both in the lagoon and in lee seaward reefs. It is ubiquitous in surge channels and competes lively in picking up fish killed by rotenone. It is not timid and approaches disconcertingly close to humans before turning away. As with *C. melanopterus*, its vision seems to be poor and its apparent boldness is probably just exploratory.

Family Orectolobidae

Species: *Ginglymostoma ferrugineum* (nurse shark)
Number examined: Eniwetok, 3 specimens: 2 empty
Sex: Males and females
Standard length: 2,100-2,500 mm

Two of the specimens were empty and the third contained partly digested remains of a rabbit fish (*Siganus* sp.). Since the nurse sharks were taken near the garbage dump, it is probable that the *Siganus* may have been dead before it was eaten. The species is a very sluggish, bottom-dwelling scavenger which rarely comes into water less than 50 ft deep. It was never seen on the reefs by us in the Marshall Islands, but a small individual was taken in shallow water in the Gilbert Islands.

Family Mobulidae

Species: *Manta alfredi* (manta ray)
Number examined: Bikini, 1 specimen
Sex: Female
Standard breadth: 2,950 mm

The stomach of this specimen contained approximately one quart of copepods and other crustacean plankters. Its planktonic feeding habits are well known. These rays were seen daily swimming about near the center of Enyu Channel, Bikini, and occasionally at various other places at Eniwetok and Arno. At Arno one approached us very closely while we were swimming just seaward of the reef margin near Ine Village, coming to within 20-30 ft of the reef edge.

Family Dussumieridae

Species: *Spratelloides delicatulus* (round herring)
Number examined: Arno, 20 specimens
Sex: Both males and females
Standard length: 20-70 mm
Digestive tract: Gill rakers very long; Y-shaped stomach; short, straight intestine.

Food item	*Percentage of fish containing the item*
Crustacea	
Copepods	85
Shrimp larvae	80
Ostracods	50
Crab zoeae	20
Mollusca	
Protoconchs	10
Polychaeta	10

This species is a typical plankton feeder, and shows a strong predilection for planktonic crustaceans. It occurs at all three atolls in very large schools on the lagoon reefs and on sheltered seaward reefs, occurring even in very shallow water just off the beaches. It is especially common around piers and ships' hulls. Tunas, belonids, and the carangid, *Scomberoides sanctipetri*, frequently are seen slashing through these dense schools of round herrings. Terns hover above the schools to catch the fish whenever they swim close to the surface.

Family Clupeidae

Species: *Harengula kunzei* (sardine)
Number examined: Arno, 20 specimens
Sex: Both males and females
Standard length: 37-82 mm.
Digestive tract: Y-shaped stomach; straight, short intestine

Food item	*Percentage of fish containing the item*
Crustacea	
Shrimp fragments	55
Ostracods	50
Copepods	15
Shrimp larvae	10
Unidentified crustacean fragments	40
Polychaeta	15
Foraminifera	
Calcarina sp.	5

This species, seen only at Arno, occurred in large schools in shallow water near the lagoon beaches. Unlike its counterpart in Japan, *H. zunasi*, which is exclusively a plankton feeder (Suyehiro 1942) taking diatoms and copepods, the Arno species is carnivorous and feeds on the shallow bottom fauna.

Family Ophichthidae

Species: *Leiuranus semicinctus* (snake eel)
Number examined: Eniwetok, 5; Bikini, 1 specimen: 5 empty
Sex: Undeveloped
Standard length: 215-490 mm
Digestive tract:short, straight intestine

The single specimen with food in its stomach contained a partly digested fossorial hemichordate, *Ptychodera* sp. It apparently feeds under the sand where it is common in areas of fine gravel-like deposits on the shallow reefs. It does not live in permanent burrows, but is capable of burying itself rather rapidly.

Species: *Brachysomophis sauropsis* (snake eel)
Number examined: Eniwetok, 2 specimens
Sex: Males
Standard length: 260-400 mm
Digestive tract: short, straight intestine

The food found in these two specimens consisted of unidentified fish fragments, a very small *Octopus* sp., several specimens of the ubiquitous foraminiferan, *Calcarina* sp., and sand grains. Like *L. semicinctus,* this species lives buried in gravelly sand without permanent burrows. It was taken commonly on all reef areas where sandy bottoms occurred. Unlike *L. semicinctus,* which has the eyes normally located on the head, *B. sauropsis* has the eyes almost at the tip of the snout, which, together with the food items taken, suggests that the latter species probably lies under the sand with just the tip of the snout protruding, keeping watch for prey inadvertently crawling or swimming close to it.

Family Muraenidae

Species: *Echidna zebra* (moray eel)
Number examined: Arno, 2 specimens
Sex: Male
Standard length: 375-575 mm
Digestive tract: teeth molariform; short, straight intestine

The specimens examined had all consumed crabs of the genus *Etisus* and other unidentified xanthids, and one contained, in addition, the crushed shell of the common reef urchin, *Echinometra mathaei.*

Species: *Echidna leucotaenia* (moray eel)
Number examined: Arno, 2 specimens
Sex: Male
Standard length: 365 mm
Digestive tract: Teeth molariform; short, straight intestine.

The specimens examined had crab fragments in their stomachs; one had fragments of a swimming crab (Portunidae) and the other contained fragments of a xanthid crab.

Species: *Echidna polyzona* (moray eel)
Number examined: Eniwetok, 1 specimen
Sex: Undeveloped
Standard length: 520 mm
Digestive tract: Teeth molariform; short, straight intestine

This specimen had consumed a large shrimp, *Saron marmoratus,* which habitually secludes itself under rocks and ledges.

Generic Summary

None of the species of *Echidna* is common, but some specimens are usually collected in extensive poison stations. All live very secretively in crevices or under rocks on the shallow reefs and are almost never seen by skindivers. Structually unique in this genus is the extensive, flattened, cobble-like dentition well adapted for crushing, rather than the shearing and stabbing teeth found in other genera of moray eels. Their prey is apparently seized as it crawls into or near the crevices in which the morays lie concealed. The sea urchin taken by one specimen is a rock dwelling species which usually is difficult to extricate from its tightly fitting depression.

Species: *Uropterygius xanthopterus* (moray eel)
Number examined: Arno, 8 specimens; 4 empty
Sex: Males and females
Standard length: 187-315 mm
Digestive tract: Teeth conical, pointed, canine-like; short straight intestine.

All four eels with food had crustacean fragments only. Three contained xanthid crab fragments and three contained alpheid shrimp fragments. This eel lives in interstices of coral mounds and masses of coralline rubble. It is strongly demersal and seldom is seen outside its place of refuge.

Species: *Rabula marshallensis* (moray eel)
Number examined: Arno, 2 specimens
Sex: Male and female
Standard length: 147-159 mm
Digestive tract: Teeth conical, pointed, canine-like; short, straight intestine

Both specimens contained fragments of small crabs. This moray lives in interstices of coral mounds and rocky debris.

Species: *Gymnothorax pictus* (moray eel)
Number examined: Arno, 4; Eniwetok, 2: 2 empty
Sex: Males and females
Standard length: 400-725 mm
Digestive tract: Teeth conical, pointed, canine-like; short, straight intestine

Of the four fish having food in their stomachs three had unidentified fish fragments and two had small crab fragments. This is the common moray found near the beach under rocks on the seaward reef flats. It is frequently encountered moving about reefs exposed by the receding tide, and commonly secludes itself under the nearest rock when startled by waders. Often it mistakes the shoes of the intruder for a rock and tries to seclude itself there, most often unsuccessfully, because humans can outrun it. Like most morays, it is vicious when teased with a stick.

Species: *Gymnothorax petelli* (moray eel)
Number examined: Arno, 14; Bikini, 1 specimen: 13 empty
Sex: Males and females
Standard length: 108-520 mm
Digestive tract: Teeth conical, pointed, canine-like; short, heavy-walled, straight intestine

Each of the two specimens containing food had crab fragments, while one had, in addition, a hippolytid shrimp, and the other contained a partly digested small fish, *Pomacentrus jenkinsi.* This comparatively small moray has habits similar to most of the others. However, it seems clear that it must feed predominantly at night, because of the small proportion of those with food in their stomachs to those without.

Species: *Gymnothorax javanicus* (moray eel)
Number examined: Arno, 4 specimens: 2 empty
Sex: Undeveloped
Standard length: 102-287 mm
Digestive tract: Teeth conical, pointed, canine-like; short, straight intestine

One of the two specimens containing food items had an alpheid shrimp, and the other contained fragments of unidentified gobies. This moray attains a very large size, some of those observed having a length of 6-7 ft. Like other morays it is seldom seen on the reefs because of its habit of secreting itself in interstices of large coral heads and coral rubble. When observed while skin-diving this eel usually has the head and forepart of the body extended from its hiding place. It is probably a night feeder.

Species: *Gymnothorax flavimarginatus* (moray eel)
Number examined: Arno, 9; Eniwetok, 2 specimens: 7 empty
Sex: Males and females
Standard length: 185-690 mm
Digestive tract: Conical, pointed, canine-like teeth; short, straight intestine

Only four of the 11 specimens examined contained food. In two of them, crab fragments were found; fragments of a blenny (*Cirripectus variolosus*), a damsel fish (*Abudefduf dicki*), and other unidentified species of fish were found in three of them. The habits of *flavimarginatus* are similar to those of *G. javanicus*, and like the latter, it also attains large sizes.

Species: *Gymnothorax buroensis* (moray eel)
Number examined: Arno, 21; Eniwetok, 4 specimens: 8 empty
Sex: Males and females
Standard length: 125-310 mm
Digestive tract: Teeth conical, pointed, canine-like; short, straight intestine

Food item	*Percentage of fish containing the item*
Crustacea	
Crab fragments, unid.	64
Xanthid crab fragments	11
Trapezia sp.	5
Shrimp fragments	8
Stomatopod fragments	5
Fish	
Fish fragments, unid.	5
Labrid, unid.	5

This is the most abundant moray on the reefs of the Marshall Islands. It is a comparatively small species which has habits similar to other morays as regards seclusion and feeding habits.

Species: *Gymnothorax undulatus* (moray eel)
Number examined: Eniwetok, 6 specimens; 4 empty
Sex: Males and females
Standard length: 600-700 mm
Digestive tract: Teeth conical, pointed, canine-like; short, straight intestine

Only two of these specimens contained food items, and these were small pomacentrids and labrids which undoubtedly had succumbed earlier to the rotenone. Like most other morays, this species probably feeds at night. It is very large and seems especially vicious. Its habits are similar to the other morays.

Species: *Gymnothorax margaritophorus* (moray eel)
Number examined: Eniwetok, 8 specimens: 4 empty
Sex: Females and undeveloped
Standard length: 160-420 mm
Digestive tract: Teeth conical, pointed, canine-like; short, straight intestine

Of the four specimens containing food, two had only gurry, another contained crustacean fragments, and the fourth contained unidentified fish fragments. This common species of the interisland reefs and seaward reef shallows does not grow large. It frequently may be found in the interstices of dead coral heads.

Species: *Gymnothorax rupelli* (moray eel)
Number examined: Eniwetok, 4 specimens: all empty
Sex: Females and undeveloped
Standard length: 300-550 mm
Digestive tract: Teeth conical, pointed, canine-like; short, straight intestine

The lack of food in the stomachs examined probably indicates a night feeding habit. However, this species appears to have habits similar to other comparatively small morays, so it doubtless feeds on crustaceans and small fish. It is particularly common on the seaward reef flats and on the interisland reefs where it hides in any crevice or under any rock available.

Species: *Gymnothorax fimbriatus* (moray eel)
Number examined: Eniwetok, 1 specimen: empty
Sex: Undeveloped
Standard length: 250 mm
Digestive tract: Teeth conical, pointed, canine-like; short, straight intestine

This moray is especially common in coral heads on the interisland reefs and leeward seaward reefs. It is a small species, frequently found when cracking open coral heads carried ashore. Its digestive tract and teeth indicate that it feeds like the other members of the genus.

Species: *Gymnothorax* sp. (moray eel)
Number examined: Bikini, 14 specimens: 7 empty
Sex: Males and females
Standard length: 230-700 mm
Digestive tract: Teeth conical, pointed, canine-like; short, straight intestine

Food item	*Percentage of fish containing the item*
Crustacea	
Odontodactylus sp.	28
Xanthid crabs, unid.	28
Etisus sp.	14
Fish	
Siganus rostratus	14
Abudefduf leucopomus	14
Unid. fragments	14
Foraminifera	
Foraminiferans and sand	14

This large moray apparently feeds also mostly by night, but a sufficient number contained food to indicate that its food and feeding habits are similar to the other morays.

Family Summary

Except for the genus *Echidna* the moray eels have very similar habits of concealment and food getting. A few become very large and are certainly the most vicious of the reef fishes, although, if unprovoked, will do little more than watch human intruders, with the head and forepart of the body protruding from a hole or crevice in the reef. Crustaceans appear to be the food type most frequently taken, doubtless because these crustaceans, like the eels, become active at night and leave their diurnal hiding places in crevices and under the sand to forage. Moray eels appear to be predominantly night feeders, as judged by the high proportion of them without food in their stomachs during the day. Small fish species which habitually remain close to coral heads and rubble are also taken commonly. The kinds of food items found suggest that morays do not forage widely, but apparently catch their prey by watchful waiting methods.

An observation made in Hawaii indicates that morays are also adept at stalking prey. One swam slowly along the edge of a rocky pool watching a lined shore crab, *Grapsus grapsus tenuicrustatus*, walking along the rock about two feet above the water's surface. Suddenly the moray slithered up the rock in pursuit of the crab, caught it and fell back into the water. Likewise, the actions of *G. pictus* slithering along on just a film of water on the seaward reef flats suggest that it seeks prey both in and out of the water.

The fang-like canine teeth, some of which are depressible, are admirably suited to predacious habits.

Family Congridae

Species: *Conger noordzieki* (conger eel)
Number examined: Arno, 4; Bikini, 1; Eniwetok, 1 specimen: 1 empty
Sex: Males and undeveloped
Standard length: 151-620 mm
Digestive tract: Teeth short, conical, very numerous and point backwards; stomach elongate, Y-shaped; intestine short, and nearly straight

Each specimen contained different food items among which were shrimp fragments, unidentified crustacean fragments, polychaete worms, unidentified fish fragments, and fish eggs. Like other eels, the conger is cryptic and is seldom seen during the day. Its night feeding forays were observed several times when the eels came into very shallow water seeking prey.

Family Moringuidae

Species: *Moringua macrochir* (whip eel)
Number examined: Arno, 20; Eniwetok, 2 specimens: 12 empty
Sex: Males and females
Standard length: 128-260 mm
Digestive tract: Short, straight intestine

Food item	*Percentage of fish containing the item*
Polychaeta	60
Foraminifera	
Calcarina sp.	40
Fish	
Unid. fragments	10
Sand	30

The whip eels are quite common in sandy bottoms of the reefs shallows on all atolls. They construct no permanent burrows, but lie below the sand completely out of sight during the day. Whip eels apparently forage for prey species just under the sand and on the bottom.

Family Synodontidae

Species: *Synodus variegatus* (lizard fish)
Number examined: Arno, 8; Bikini, 4; Eniwetok, 5 specimens: 10 empty
Sex: Males and females
Standard length: 72-220 mm
Digestive tract: Teeth canine-like, numerous on both jaws and tongue; stomach heavy-walled; intestine short, straight

Food item	*Percentage of fish containing the item*
Fish	
Unid. fragments	71
Epinephelus sp.	14
Abudefduf sp.	14

Five specimens collected at Eniwetok had picked up recently poisoned fish and were considered as empty for this study. This species is ubiquitous on sandy patches in all reefs areas. It lies mostly buried in the sand, with only the eyes and forepart of the head exposed watching for prey which may venture too closely. It is obliteratively colored for sandy bottom, so that its habit of lying perfectly motionless until it darts out after its victim is very effective. It is a voracious, small carnivore.

Species: *Saurida gracilis* (lizard fish)
Number examined: Arno, 16 specimens: 4 empty
Sex: Males and undeveloped
Standard length: 45-131 mm
Digestive tract: Teeth canine-like in profusion on both jaws, palatines, vomer, and tongue; teeth on jaws not covered by lips; stomach heavy-walled; intestine short, straight

Food item	*Percentage of fish containing the item*
Fish	
Unid. fragments	67
Unid. juvenile fish	17
Apogon novemfasciatus	8
Allanetta ovalaua	8
Fish scales	8

This species is distributed widely about all reefs, and has habits very similar to *Synodus variegatus*.

Family Summary

Lizard fish have obliterative color patterns so that when they lie motionless on sandy bottoms, or are partially buried in the sand, they are virtually impossible to detect. When prey species, mostly small fish, come within a few feet of them they dart upward very rapidly and seize their victim. Rarely have they been observed to swim more than 3-4 ft upward while attacking prey species. The profuse and powerful canine-like dentition provides a very effective mechanism for catching small fish. Our analyses and observations indicate that only fish were taken as food. However, Suyehiro (1942) reports that *Saurida undosquamis* in Japan will take shrimps and squid in addition to its more usual diet of small fish.

Family Belonidae

Species: *Strongylura gigantea* (needle fish; "Gar fish")
Number examined: Eniwetok, 2 specimens: both empty
Sex: Male and female
Standard length: 840-1,030 mm
Digestive tract: Jaws extremely long and needle-like toward the tip, mouth large, teeth canine-like arranged in villiform bands with inner row of enlarged canines; alimentary tract a straight, heavy-walled tube divided into an oesophagus and intestine, no stomach.

Both specimens examined had been caught by hook and line near the garbage dump, and one contained only garbage in its stomach. Observations indicate that this surface swimming species is a voracious carnivore, feeding on small fish by drifting up to them and then suddenly lashing out with its jaws.

Species: *Strongylura incisa* (needle fish)
Number examined: Arno, 1 specimen
Sex: Undeveloped
Standard length: 143 mm
Digestive tract: Jaws and teeth similar to *S. gigantea*; alimentary tract a straight tube, no stomach.

This specimen, a very small one, contained a small fish, *Allanetta ovalaua*.

Family Summary

Members of the Family Belonidae apparently feed by drifting into schools of fish or crustaceans (Randall 1955), whereupon they suddenly lash out with their long, tooth-lined jaws to capture their prey. In our observations, and in those of Al=Hussaini (1947), small schooling species such as round herrings and silversides were most often the object of these carnivores which travel in small schools just below the surface. However, Suyehiro (1942) mentions that a closely related species in Japan, *Athlennes anastomella*, contained the remains of a rather large fish. Japanese fishermen also report that this species uses its long, powerful jaws very effectively in attacking larger prey species.

Family Hemiramphidae

Species: *Hyporhamphus laticeps* (halfbeak)
Number examined: Bikini, 8; Eniwetok, 12 specimens: 1 empty
Sex: Males and females
Standard length: 215-320 mm
Digestive tract: Lower jaw elongate and pointed, upper jaw short, teeth in both jaws minute, mouth large; a straight tube from the oesophagus to the anus, no stomach

Food item	*Percentage of fish containing the item*
Fish	
Unid. small fish (probably round herrings)	47
Crustacea	
Shrimp larvae	21
Mysids	15
Shrimp fragments	10
Crab zoeae	5
Polychaeta	
Unid. swimming polychaetes	26

This species swims in midwater or near the surface in small schools on all reefs investigated. It is a small, midwater carnivore which feeds on whatever prey species are available, showing comparatively little predilection for small fish species over swimming crustaceans or polychaetes.

Species: *Hyporhamphus affinis* (halfbeak)
Number examined: Arno, 16 specimens: 3 empty
Sex: Unknown
Standard length: Unmeasured
Digestive tract: Similar to *H. laticeps*

Food item	*Percentage of fish containing the item*
Crustacea	
Copepods	30
Crab zoeae	23
Crab fragments	15
Fish	
Unid. fragments	30
Foraminifera	
Several pelagic species	30
Gastropoda	
Veliger larvae	8
Gurry	23

This species apparently feeds predominantly on plankton, but it is capable also of taking small fish.

Family Summary

The halfbeaks are comparatively small, mid-water and surface dwellers where they occur in rather large schools. Younger individuals are primarily zooplankton feeders, but as they become larger their predilection turns to small, densely schooling surface fishes such as round herrings and silversides.

Earlier accounts (Jordan 1907) suggest that the halfbeaks are phytoplankton feeders, but this seems to be in error as our studies, as well as those of Uchida, reported by Suyehiro (1942), indicate that they are carnivores. No particular function can be ascribed to the elongate lower jaw by us, although it may be used to stun small fishes by a slashing action. Uchida believes that not only is the lower jaw useless when taking food, but actually is a hindrance.

Family Bothidae

Species: *Bothus mancus* (flounder)
Number examined: Arno, 5; Bikini, 6; Eniwetok, 12 specimens: 4 empty
Sex: Males and females
Standard length: 97-300 mm
Digestive tract: Short, nearly straight intestine

Food item	*Percentage of fish containing the item*
Fish	
Unid. gobies	21
Unid. fragments	21
Acanthurus t. triostegus (juvenile)	10
Unid. balistid (juvenile)	10
Unid. labrid	10
Parupeneus trifasciatus	5
Ctenogobius sp.	5
Abudefduf amabilis	5
Pomacentrid (juvenile)	5
Apogon novemfasciatus	5
A. erythrinus	5
Istiblennius pavlus	5
Tripterygion minutus	5
Crustacea	
Odontodactylus sp.	15
Trapezia sp.	10
Thalamita sp. fragments	10
Portunid fragments	5
Xanthid crab fragments	5
Palaemonid shrimp fragments	5
Amphipod	5

With a very effective obliteratively colored upper surface this flounder lies motionless on rocks or sandy bottoms on all reefs studied. At times it covers itself, except for the eyes, with sand, thus becoming almost impossible to discern. After thus lying in wait for prey species to venture close enough, it seizes any fish or crustacean possible for it to ingest. Insofar as we could ascertain it responds only to moving prey. All the food items taken are species which frequent the bottom in sandy areas adjacent to coral mounds or rubble.

Family Holocentridae

Species: *Myripristis berndti* (squirrel fish)
Number examined: Arno, 7 specimens: 2 empty
Sex: Females and undeveloped
Standard length: 40-99 mm
Digestive tract: Teeth short, rather weak; stomach moderately heavy-walled; intestine short, straight

All five of the specimens containing food had only fragments of shrimps. This species and all other holocentrids examined had very little food in their stomachs, which is to be expected, since they are well known night feeders. All specimens of this species examined by Randall (1955) in the Gilbert Islands were empty of food.

Species: *Myripristis microphthalmus* (squirrel fish)
Number examined: Eniwetok, 17 specimens: 5 empty
Sex: Males and females
Standard length: 135-170 mm
Digestive tract: Similar to *M. berndti*

Food item	*Percentage of fish containing the item*
Crustacea	
Unid. crab fragments	58
Portunid crabs	16
Crab megalopa	8
Crab zoeae	8
Unid. shrimps	25
Alpheid shrimp	8
Stomatopod fragments	16
Galathea sp.	8
Amphipods	8
Polychaeta	
Unid. tube dwellers in sand near coral mound	16
Algae	
Turbinaria sp. tips	8
Sand grains	8

This species takes a great variety of crustaceans which are associated with, or swim near, the coral mounds in which this spelean fish secludes itself. Two specimens had the gut filled with hundreds of polychaetes which inhabit membranous tubes forming a dense network just beneath the surface of the rather compacted sandy bottoms on the protected lagoon reefs. The lack of sand in the gut indicates that the worms were pulled from their tubes, rather than being excavated from the sand by rooting actions of the fish.

Species: *Myripristis* sp. (squirrel fish)
Number examined: Bikini, 7 specimens: 5 empty
Sex: Males and females
Standard length: 70-210 mm
Digestive tract: Similar to *M. berndti*

Stomach contents of the two specimens containing food consisted of the following crustaceans: *Odontodactylus* sp., inachid crab fragments, and amphipods; and the following small fish: *Ctenochaetus striatus*, labrids, and unidentified larval stages.

Species: *Holocentrus sammara* (squirrel fish)
Number examined: Arno, 5; Eniwetok, 8 specimens: 2 empty
Sex: Males and females
Standard length: 34-165 mm
Digestive tract: Teeth short, weak; stomach moderately heavy-walled; intestine medium in length with one loop.

Food item	*Percentage of fish containing the item*
Crustacea	
Crab fragments	36
Parthenopiid crab	27
Thalamita sp.	18
Pachygrapsus plicatus	9
Portunid crab	9
Maiid crab	9
Unid. crustacean fragments	18
Copepods	9
Coelenterata	
Pieces of unid. coral, partly digested	18
Polychaeta	
Unid. polychaetes	9
Gastropoda	
Cerithium sp.	9
Algae	
Algal frond, bitten off	9

This species, like other squirrel fish, hides under rocks or in small coral caverns during the day, and feeds primarily at night. However, it is the most commonly observed squirrel fish during the day, as it frequently comes out of its hiding place and seems less secretive than the others.

Species: *Holocentrus lacteoguttatus* (squirrel fish)
Number examined: Arno, 4 specimens: 1 empty
Sex: Females
Standard length: 59-82 mm
Digestive tract: Similar to *H. sammara*

Shrimp fragments, small gastropods, and gurry were found in the three specimens containing food in their stomachs.

Species: *Holocentrus microstomus* (squirrel fish)
Number examined: Arno, 24; Eniwetok, 5 specimens: 3 empty
Sex: Males and females
Standard length: 45-191 mm
Digestive tract: Similar to *H. sammara*

Food item	*Percentage of fish containing the item*
Crustacea	
Crab fragments	42
Shrimp fragments	23
Alpheid shrimp	6
Gonodactylus sp.	3
Fish	
Unid. fragments	15
Chromis caeruleus	3
Gastropoda	
Small unid. gastropods	3
Coelenterata	
Hydroid fragments	3
Polychaeta	
Unid. polychaetes	3
Gurry	6

Species: *Holocentrus laevis* (squirrel fish)
Number examined: Eniwetok, 4 specimens: 1 empty
Sex: Males and females
Standard length: 125-150 mm
Digestive tract: Similar to *H. sammara*

In the three fish containing food in their stomachs the following crustaceans were found: crab fragments, a portunid crab, a maiid crab, and shrimp fragments.

Species: *Holocentrus diadema* (squirrel fish)
Number examined: Eniwetok, 14 specimens: 1 empty
Sex: Males and undeveloped
Standard length: 75-120 mm
Digestive tract: Similar to *H. sammara*

Food item	*Percentage of fish containing the item*
Gastropoda	
Atys sp.	46
Unid. gastropods	14
Polychaeta	
Unid. polychaetes	46
Crustacea	
Xanthid crab fragments	38
Isopods	23
Unid. fragments	14
Shrimp fragments	7
Alpheid shrimp	7
Pelecypoda	
Small coral-dwelling clams	14
Amphineura	
Solenogastrid	7

Species: *Holocentrus spinifer* (squirrel fish)
Number examined: Eniwetok, 9 specimens: 1 empty
Sex: Males and females
Standard length: 150-280 mm
Digestive tract: Similar to *H. sammara*

Food item	*Percentage of fish containing the item*
Crustacea	
Xanthid crabs	50
Charybdis sp.	12
Portunid crab	12
Maiid crab	12
Stomatopod	12
Fish	
Unid. fragments	12

Species: *Holocentrus* sp. (squirrel fish)
Specimens examined: Bikini, 5 specimens
Sex: Males and females
Standard length: 80-140 mm
Digestive tract: Similar to *H. sammara*

Three of the five specimens contained only fragments of the small coral crab, *Trapezia* sp., while the remaining two specimens contained only shrimp fragments.

Family Summary

Food and feeding habits of all members of this family appear to be very similar. All are carnivores, taking a wide variety of crustaceans, polychaetes, small fish, and gastropods. During the day squirrel fish are cryptic, secluding themselves to a great extent in holes, under ledges, or in larger caverns in coral mounds or rubble. All have comparatively large eyes, and feed almost exclusively at night. Food remains are infrequent in the stomachs during the day, persistent items being generally the hard parts of prey taken the previous night. In many instances the intestines had to be searched for traces of food items because the stomachs were empty. Randall (1955) reported that most of the stomachs of holocentrids in the Gilbert Islands were also empty, and those containing food had remains of crustaceans and small fish.

The fact that many of the squirrel fish contained polychaetes which were tube dwellers on sandy bottoms indicates that they do forage well away from their day time hiding places. None were observed feeding on these polychaetes during daylight hours. Further evidence of their foraging on sand bottoms is shown by the presence of sand dwelling gastropods (*Atys* sp.) and the fossorial solenogastrid amphineurans. The few broken, partly digested tips of coral branches in the stomach of *H. sammara* may have been taken inadvertently while the fish was seeking small crabs wedged in interstices. We do not believe that any holocentrid feeds habitually on living coral.

Family Syngnathidae

Species: *Corythoichthys flavofasciatus conspicillatus* (pipefish)
Number examined: Eniwetok, 3 specimens
Sex: Males and females
Standard length: 82-95 mm
Digestive tract: Snout long, pipette-like; mouth cavity small, teeth absent; alimentary canal straight, no stomach.

All three pipefish examined contained copepods; one had, in addition, some small isopods, and another had taken several ostracods along with the copepods. This pipefish is very common on all reefs studied in the northern Marshalls, and frequently is seen lying on coral heads, rubble, or sand.

Species: *Corythoichthys intestinalis waitei* (pipefish)
Number examined: Arno, 1 specimen
Sex: Female
Standard length: 85 mm
Digestive tract: Similar to *C. f. conspicillatus*

This specimen contained copepods, copepod nauplii, and ostracods in about equal abundance. Although this pipefish was not seen at either Eniwetok or Bikini, it was locally abundant at Arno and Majuro Atolls in the southern Marshalls. Its habits are very much like those of *C. f. conspicillatus.*

Generic Summary

The food getting structures and the food items eaten by the two species of *Corythoichthys* suggest that these pipefish probably use their snout as a sort of pipette to take up minute crustaceans so abundant on the surface of coral rubble and compacted sand bottoms. Al= Hussaini (1947) suggests that the pipefishes take mostly planktonic crustaceans, but we believe that the species ingested are benthonic. There is no evidence that the snout is distensible or that they can swallow prey larger than might be expected, as Bigelow & Welsh (1924) have described for the related species *Siphostoma fuscum* of the east coast of North America.

Family Aulostomidae

Species: *Aulostomus chinensis* (trumpet fish)
Number examined: Eniwetok, 1 specimen
Sex: Female
Standard length: 600 mm
Digestive tract: Snout very long, tubular, with jaws at end, mouth capable of bellows-like dilation; intestine short, straight

The single specimen examined was taken by spear, and contained a small silverside (Atherinidae) in its stomach. Because rotenone was not used it appears likely that the silverside was a normal dietary item. This solitary trumpet fish has frequently been observed to swim slowly over open areas and near coral heads and rubble. It appears to glide about, seldom seeking cover. Although it has never been seen to capture food, its structural features suggest that it captures small prey by a rapid dilation of its mouth, particularly prey secluded in shallow holes or interstices into which it could probe with its long, tubular snout.

Family Fistulariidae

Species: *Fistularia petimba* (cornet fish)
Number examined: Bikini, 9 specimens
Sex: Males and females
Standard length: 500-700 mm
Digestive tract: Snout, long, tubular, jaws at end, very short and with an extremely small mouth opening, but capable of being broadened or narrowed, teeth small; alimentary tract straight.

Food item	*Percentage of fish containing the item*
Fish	
Labrids	77
Pomacentrids	33
Unid. small fish	33
A. t. triostegus	11
Balistids	11

This cornet fish occurs rather commonly in schools swimming near the surface, and occasionally in mid-water or near the bottom, in the quiet waters of the lagoon reef and leeward sea reefs. Frequently the schools lie quite motionless. It is obvious from the food items found that they frequent the vicinity of coral heads as well as cruise over the reef flats, and that they are capable of taking small fishes which are larger than the mouth opening of dead specimens. Hence, the extension of its flute-like snout is very important. We cannot agree with Suyehiro (1942) that this species takes only minute, floating creatures by utilizing its snout as a pipette. Our specimens contained nothing but small fish, although it is certain that swimming crustaceans, etc., would be taken if available. One of us has seen the species taken on a large bass plug in Hawaii.

Family Atherinidae

Species: *Stenatherina temmincki* (silverside)
Number examined: Bikini, 8 specimens: 1 empty
Sex: Males and females
Standard length: 85 mm
Digestive tract: Mouth moderately large, teeth weak; stomach absent, intestine moderately short, one loose coil

Food item	*Percentage of fish containing the item*
Crustacea	
Shrimp larvae	57
Copepods	28
Stomatopod larvae	14
Foraminifera and sand	57
Gastropoda	
Unid. small species	14
Fish	
Unid. fragments	14

This species occurs in very large schools near the surface or in mid-water. Some have been observed feeding from the bottom in very shallow water. Thus, observations as well as an analysis of the food items ingested indicate that this silverside feeds both on planktonic and benthonic forms.

Species: *Allanetta ovalaua* (silverside)
Number examined: Arno, 12 specimens: 3 empty
Sex: Males and females
Standard length: 66-74 mm
Digestive tract: Similar to *S. temmincki*

Food item	*Percentage of fish containing the item*
Crustacea	
Calanoid copepods	88
Crab zoeae	44
Gastropoda	
Veliger larvae	11

This species swims near the surface and in mid-water in very large schools on all reefs visited. It behaves primarily as a selective feeder on zooplankton.

Species: *Pranesus pinguis* (silverside)
Number examined: Arno, 5 specimens: 3 empty
Sex: Males and females
Standard length: 66-74 mm
Digestive tract: Similar to *S. temmincki*

Both specimens containing food items had copepods and crab zoeae. This species has habits similar to *A. ovalaua*, and is often found schooling with that species.

Family Summary

Atherinids are ubiquitous in large schools on virtually all reefs visited. For the most part they subsist on zooplankton, being rather selective in that they take mostly crustaceans and larval gastropods. At least one species, *S. temmincki,* feeds on the benthonic types of minute organisms when the school moves into very shallow, protected areas of the reefs.

Family Mugilidae

Species: *Neomyxus chaptali* (mullet)
Number examined: Bikini, 3 specimens
Sex: Males and females
Standard length: 160-190 mm
Digestive tract: Teeth trifid setiform; stomach heavy-walled, but not gizzard-like; intestine very long, coiled

The three specimens examined all contained diatoms, desmids, and fine filamentous algae, some foraminiferans and detritus. This species apparently strains sandy bottom material from which it gets the minute algal forms and, perhaps only by inadvertence, picks up some minute animal species from the surface of the substrate.

Species: *Crenimugil crenilabis* (mullet)
Number examined: Arno, 11; Eniwetok, 2 specimens
Sex: Females and undeveloped
Standard length: 112-400 mm
Digestive tract: Stomach heavy-walled and a gizzard, but less heavy and with a greater lumen than in *Mugil cephalus;* intestine very long, coiled

Food item	*Percentage of fish containing the item*
Detritus and sand (fine)	92
Algae	
Oscillatoria sp.	84
Diatoms (*Nitzschia* sp. mostly)	61
Fine filamentous algae (appears scraped from compacted sandy bottoms)	15
Foraminifera	76

This species feeds quite similarly to the well known gray mullet, *Mugil cephalus*, except that larger items pass into the gut of *C. crenilabis.* It is frequently solitary or forms small schools in the less turbulent waters of the lagoon and seaward reefs. It is often seen feeding in very shallow water on compacted sandy or muddy bottoms.

Family Summary

Probably as much has been written about the digestive tract and food habits of the mullet as for any other group of fishes. The peculiar digestive tract of *Mugil cephalus* has been reported on in detail by many writers, since Cuvier and Valenciennes described it in the early nineteenth century. More recently Ghazzawi (1933, 1935) studied both morphological and histological features as well as the feeding habits of *M. cephalus* and *M. capito* in Egypt, and Al=Hussaini (1947) reported on a similar study for *M. auratus;* Suyehiro (1942) did likewise for *M. cephalus* in Japan; and Hiatt (1947a) described feeding habits and alimentary tract morphology for *M. cephalus* in Hawaii. All agree that mullets feed predominantly on unicellular algae composing the benthos. Inadvertently, perhaps, they also ingest a considerable amount of the microfauna associated with the same habitat. The exceptionally long intestine and the triturating gizzard containing fine sand as an abrasive are evidence of mullets' primary dependence upon such forms as diatoms and desmids.

Family Sphyraenidae

Species: *Sphyraena qenie* (barracuda)
Number examined: Eniwetok, 2 specimens: both empty
Sex: Female
Standard length: 1,220-1,240 mm
Digestive tract: Mouth large, pointed; large canine teeth; intestine short, straight

Both specimens examined were caught by hook and line near the garbage dump, and had no natural food items in their stomachs. Although this species is uncommon in the Marshall Islands it has been observed several times drifting solitarily near the surface stalking its prey. It surprises its victim with a sudden lunge. Barracuda probably also feed at mid-depth or near the bottom. Its main food is undoubtedly fish.

Family Polynemidae

Species: *Polydactylus sexfilis* (threadfin)
Number examined: Arno, 18 specimens: 12 empty
Sex: Undeveloped
Standard length: 57-86 mm
Digestive tract: Moderately short intestine

Food item	*Percentage of fish containing the item*
Crustacea	
Shrimp fragments	50
Crab fragments	33
Polychaeta	16
Foraminifera	
Calcarina sp.	16

Small specimens of this schooling species are found commonly on the reef shallows over sandy bottoms in protected areas. Larger fish are found along sandy beaches where the surf is rather strong. It feeds strictly on the benthonic fauna.

Family Scombridae

Species: *Gymnosarda nuda* (dogtooth tuna)
Number examined: Eniwetok, 2 specimens: both empty
Sex: Unknown
Standard length: 44-45 inches
Digestive tract: Several conical, pointed, canine-like teeth in jaws; stomach thick-walled; intestine short, almost straight

Neither of these specimens, caught by hook and line near a pass in the Eniwetok lagoon, had food in their stomachs, although others were often seen in small schools slashing through the dense schools of round herring near the pier. This species seems to swim more deeply than species of either *Katsuwonus* or *Euthynnus* which also occur inside the lagoons and in the surrounding seas. Dogtooth tuna are pelagic, rapid-swimming carnivores which grow to a large size. Woods (1953) mentions that this species had taken scads (*Decapterus muroadsi*) in the northern Marshalls, and the senior author noted the stomachs of this species at Bikini to contain scads (*Decapterus sanctaehelenae*) as well as pelagic squid, flying fishes, and other small schooling types (Hiatt & Brock 1948).

Species: *Euthynnus affinis yaito* (little tunny)
Number examined: Observations only

No specimens of this species were available for food analysis, but small schools were observed repeatedly at

Eniwetok to slash through the dense schools of round herrings swimming near the pier. It is a rapid swimming, schooling, pelagic carnivore which feeds most often near the surface. It is known to take small fish, pelagic crustaceans, and pelagic squid (Welch 1950). The senior author has observed this species feeding among a dense school of atherinids at Arno which had surrounded him while skin-diving near the outer slope of the lagoon reef. The tunnys showed no concern whatever for the swimmer while slashing with great speed through the silversides, frequently as close as 5-6 ft from him. In another instance three medium-sized tunnys were observed herding a large school of several hundred scads, *Decapterus sanctaehelenae*, over a large coral knoll for over three hours in Rongerik Atoll in the northern Marshall Islands (Hiatt & Brock 1948). One lagging scad was captured by one of the tunnys. The entire performance was extraordinary, but probably typical, as Kishinouye (1923) also reports, although he singles this species out among the bonitos as the one which does not engage in herding prey.

Species: *Katsuwonus pelamis* (oceanic skipjack)
Number examined: Observations only

As with the other tunas reported herein, this schooling species was observed to slash repeatedly through the dense school of round herrings around the pier at Eniwetok. Because of its great economic importance and wide range the food and feeding habits of this species have been studied intensively. In Hawaii, Welch (1950) reports that this species subsists mainly on cephalopods, stomatopod larvae, and small fish, while Suyehiro (1942) and others in Japan have found this genus to feed principally on small or juvenile fishes, cuttle-fish, shrimps, schizopods, and amphipods.

Family Summary

The tunas are large, pelagic, fast-swimming, schooling carnivores which take virtually any prey of the proper size. Because of their pelagic nature, the food of those caught at sea consists mainly of schooling fishes, crustaceans, and squid which they capture by visual means. Those taken in lagoons or close to land appear to contain larval fishes and crustaceans which are produced by reef-and shore-dwelling adults. This type of food, supplementing the usual high seas forage species, probably is significant in attracting tunas close to mid-ocean islands.

Family Carangidae

Species: *Trachurops crumenophthalmus* (scad)
Number examined: Arno, 23; Bikini, 1; Eniwetok, 3 specimens: 4 empty
Sex: Males and females
Standard length: 85-245 mm
Digestive tract: Mouth moderately large, teeth small; stomach rather thick-walled; intestine rather short, with one loop

Food item	*Percentage of fish containing the item*
Foraminifera	
Calcarina sp.	47
Marginopora sp.	13
Gastropoda	
Cerithium sp.	26
Unid. small gastropods	17
Fish	
Unid. fragments	17
Crustacea	
Pelagic shrimps	8
Miscellaneous items	
Sand grains	30
Pebbles	26
Gurry	21

All specimens containing food were juvenile fish taken at Arno Atoll where they formed large schools which frequented the protected lagoon reef and inter-island reefs. Unlike most carangids (and this is perhaps an age characteristic) these scads fed principally on the benthonic fauna of the reef shallows, particularly the forms occurring on compacted sand. In all cases the foraminiferans eaten were enveloped in a viscous fluid which was probably associated with the digestive process. The adults of a closely related species in Japan, *Decapterus muroadsi*, were found by Suyehiro (1942) to have taken mostly larval fishes.

Species: *Trachinotus bailloni* (pompano)
Number examined: Arno, 9 specimens: 4 empty
Sex: Undeveloped
Standard length: 56-101 mm
Digestive tract: Mouth small; stomach thick-walled; intestine moderately short

Food item	*Percentage of fish containing the item*
Fish	
Unid. fragments	100
T. bailloni, juveniles	20
Crustacea	
Isopods	20
Crab fragments	20

This species is a slow-cruising carnivore which occurs in pairs or small schools. It lives rather close to shore in the lagoon shallows. The specimens examined were all juveniles, so the food of the adult of this pompano is unknown, but fish probably predominate in their diet as they do with the juveniles.

Species: *Carangoides ferdau jordani* (jack)
Number examined: Arno, 2; Eniwetok, 3 specimens: 2 empty
Sex: Males and females
Standard length: 250-395 mm
Digestive tract: Intestine short, straight

The three specimens containing food had eaten the following fish: *Bathygobius f. fuscus*, *Parupeneus trifasciatus*, unidentified goby, and unidentified fish fragments. This species grows rather large, and is a fast-swimming, roving carnivore on all reefs visited. It sometimes is seen schooling with other types of fish.

Species: *Caranx melampygus* (jack)
Number examined: Arno, 1; Eniwetok, 1 specimen
Sex: Females
Standard length: 555 mm
Digestive tract: Intestine very short, straight

One specimen contained a small scad, *Trachurops crumenophthalmus*, and the other an unidentified fish fragment. This species, like *Carangoides ferdau jordani*, is a large, rapid-swimming, roving carnivore which prefers reef areas with considerable open water, either in lagoons, or in surge channels of the seaward reefs. It apparently feeds in mid-water close to coral mounds where it catches small coral-dwelling fish. In the Gilbert Islands Randall (1955) found the species to take coral-dwelling fish such as small wrasses.

Species: *Caranx lessoni* (jack)
Number examined: Eniwetok, 1 specimen: empty
Sex: Female
Standard length: 640 mm
Digestive tract: Intestine very short, straight

The single specimen was empty, but its observed habits are very much like *C. melampygus*.

Species: *Elagatis bipinnulatus* (rainbow runner)
Number examined: Eniwetok, 2 specimens: 1 empty
Sex: Male and female
Standard length: 535-590 mm
Digestive tract: Mouth comparatively small, teeth in villiform bands; intestine short

The one specimen containing food in its stomach had a pelagic shrimp, a crab megalops, and some unidentified fish fragments. This species is a fast-swimming carnivore which is more or less pelagic. It is abundant around the pier at Eniwetok where it may be chummed to the surface easily. At intervals small schools of 5-10 individuals slash through the dense school of round herring near the pier. Its usual food is probably pelagic fish although it certainly will take swimming crustaceans or squid.

Family Summary

Many differences in feeding methods and predilections for food items occur among the several genera in this family, although all are carnivores. The smaller species, e.g., scads, frequently forage for benthonic fauna in very shallow water, although adult scads are seen most often in large schools in mid-water where they doubtless take small fish and pelagic invertebrates. The larger carangids, e.g., *Trachinotus, Carangoides,* and *Caranx,* feed mostly as roving carnivores, with *Trachinotus* inhabiting the more open water in small schools, and the other two genera inhabiting reef shallows and channels, mostly in a solitary fashion, where they feed upon small fish associated with the coral heads. They typically inhabit the deeper water just off the seaward reef edge during low tides, and move up onto the reef proper when the tide rises. *Elegatis bipinnulatus* is more pelagic than the other species and occupies a mid-water or surface position, usually in small schools. The small mouth suggests that only very small pelagic fishes and swimming crustaceans serve them as food.

Although no specimens were collected for examination, three separate observations of the jack, *Gnathanodon speciosus,* two at Arno, and one at Eniwetok are worthy of reporting. At Arno two fish of this species were observed swimming along-side the head of a large white-tipped shark, *Triaenodon obesus,* near the outer edge of the lagoon reef, at Eniwetok one fish was seen hovering about the head of a large nurse shark, *Ginglymostoma ferrugineum,* and three were observed at very close range swimming about the head of a giant sea bass, *Promicrops lanceolatus.* In no case were the sharks or the bass following the brilliantly yellow and black barred carangid, but the latter remained close to the head of the larger fish at all times.

The larger carangids are certainly one of the most important of the roving carnivores over all Marshallese reefs.

Family Apogonidae

Species: *Apogon novemfasciatus* (cardinal fish)
Number examined: Arno, 21; Bikini, 3 specimens: 7 empty
Sex: Males and females
Standard length: 34-70 mm
Digestive tract: Mouth large, small villiform teeth; stomach large, Y-shaped; intestine moderately short with one loop

Food item	*Percentage of fish containing the item*
Fish	
Unid. fragments	35
Damsel fish	11
Wrasses	11
Unid. gobies	11
Bathygobius f. fuscus	5
Amphiprion melanopus	5
Apogon frenatus	5
Fish eggs	11
Crustacea	
Shrimp fragments	17
Xanthid crab fragments	17

This species is perhaps the most ubiquitous cardinal fish in the Marshall Islands. It lives beneath ledges or in caverns in rather large coral heads, and often aggregates into loose schools of several individuals. It is a voracious carnivore taking fish and crustaceans closely associated with the same coral head. These apogonids have never been observed more than a few feet away from their hiding place.

Species: *Apogon snyderi* (cardinal fish)
Number examined: Arno, 6; Bikini, 4; Eniwetok, 11 specimens: 3 empty
Sex: Males and females
Standard length: 54-110 mm
Digestive tract: Similar to *A. novemfasciatus*

Food item	*Percentage of fish containing the item*
Crustacea	
Shrimp fragments	38
Xanthid crabs	22
Ostracods	11
Copepods	5
Alpheus sp.	5
Isopods	5
Fish	
Unid. fragments	27
Gastropoda	
Cerithium sp.	5

This solitary species lives mostly around coral mounds on the lagoon reefs near the outer slope at depths of 10-15 ft; but some have been taken in protected ocean reef shallows. It dwells in crevices and caverns in the coral, and subsists mainly on small fish and crustaceans in the immediate vicinity of its hiding place. Randall (1955) found this species to have taken small fish and crustaceans in the Gilbert Islands.

Species: *Apogon exostigma* (cardinal fish)
Number examined: Arno, 5 specimens: 1 empty
Sex: Females
Standard length: 45-53 mm
Digestive tract: Similar to *A. novemfasciatus*

Food item	*Percentage of fish containing the item*
Crustacea	
Xanthid crab fragments	50
Fish	
Eviota sp.	25
Polychaeta	25

Species: *Apogon nigrofasciatus* (cardinal fish)
Number examined: Eniwetok, 3 specimens
Sex: Female and undeveloped
Standard length: 52-68 mm
Digestive tract: Similar to *A. novemfasciatus*

Two of the specimens examined contained unidentified shrimps; one contained, in addition, and unidentified polychaete. The remaining specimen contained an alpheid shrimp. This species is common on both the seaward reef shallows and on the lagoon reefs, living under ledges and in interstices of coral mounds. Its food consists of items closely associated with the same coral heads.

Species: *Apogon novaeguineae* (cardinal fish)
Number examined: Eniwetok, 2 specimens
Sex: Undeveloped
Standard length: 36-41 mm
Digestive tract: Similar to *A. novemfasciatus*

Both specimens examined had taken shrimp, and one had, in addition, the abundant foraminiferan, *Calcarina* sp. This species, common both on seaward and lagoon reefs, in crevices and holes in coral mounds, is sometimes found in close association with echinoids. The foraminiferan in one specimen suggests that at times it feeds on benthonic fauna.

Species: *Apogon erythrinus* (cardinal fish)
Number examined: Eniwetok, 1 specimen
Sex: Female
Standard length: 34 mm
Digestive tract: Similar to *A. novemfasciatus*

This specimen contained unidentified fish fragments and an unidentified polychaete. This species is common about crevices and caves in coral mounds on both seaward and lagoon reefs down to depths of at least 18 feet.

Species: *Apogon* sp. (cardinal fish)
Number examined: Bikini, 3 specimens
Sex: Males and females
Standard length: 85-90 mm
Digestive tract: Similar to *A. novemfasciatus*

All specimens contained remains of shrimps, one an alpheid shrimp, another a *Leander* sp., and the third had unidentified shrimp fragments.

Species: *Gymnapogon philippinus* (cardinal fish)
Number examined: Arno, 3 specimens: 2 empty
Sex: Females
Standard length: 35-40 mm
Digestive tract: Mouth large, teeth erect, large canine teeth on vomer; intestine short

The single fish with food items in its stomach contained fish eggs. We cannot be certain that these are not eggs of this species which may have been "incubating" in the mouth of the fish, as some of the cardinal fish are known to do. Its large canines suggest that it is a voracious carnivore. This species lives beneath ledges and in interstices of living or dead coral heads, particularly on the protected seaward reefs. It has never been seen alive by the authors, despite many hours of intensive observation in its habitat. Thus, it is probably very secretive during the day and forages at night. The empty stomachs add evidence to this suggestion.

Species: *Paramia quinquelineata* (cardinal fish)
Number examined: Arno, 8 specimens
Sex: Males and females
Standard length: 36-55 mm
Digestive tract: Mouth large, canines weak; intestine short

Food item	*Percentage of fish containing the item*
Fish	
Unid. fragments	37
Eviota sp.	12
Wrasses	12
Crustacea	
Shrimp fragments	25
Crab fragments	12
Gastropoda	
Atys sp.	12

This species is very shy, seldom seen, and lives under ledges and in caves, rarely in interstices of coral heads. It apparently forages on the benthonic fauna of sandy areas adjacent to its hiding place, as the eleotrid, *Eviota* sp., and the gastropod, *Atys* sp., are benthonic, sandy-substrate dwellers.

Species: *Cheilodipterus macrodon* (cardinal fish)
Number examined: Bikini, 1 specimen
Sex: Male
Standard length: 90 mm
Digestive tract: Mouth large, numerous fang-like canines in jaws; intestine short.

The single specimen examined had eaten a blenny, *Istiblennius* sp. This species was common in the deeper reef areas of the lagoon at Bikini, but uncommon or rare in a similar habitat at Eniwetok. It is solitary and lives under ledges near mounds of rubble or living coral. This species is one of the largest apogonids in the Marshall Islands.

Family Summary

The cardinal fishes all have rather similar habits, although the dental armature varies appreciably among the several genera found in the Marshall Islands. All are voracious carnivores, taking fish, crustaceans, and other invertebrates if they are of the proper size. Suyehiro (1942) reports that *Apogon lineatus* and *A. semilineatus* of Japan take small crustacea and larval fish. Suyehiro also points out an interesting situation, with which our observations also agree, that when the ovaries are well developed the females cease to take food. We found this to be the case with every species in which the females had eggs nearing maturity. Most species apparently forage diurnally, although at least one species appears to be a nocturnal feeder.

Ordinarily cardinal fishes occur solitarily, or in rather small schools, although some species not covered in this study form dense schools over and in patches of certain living, branching corals, and others form large schools confined to coral mounds with large caverns in which they hide if disturbed. *A. novaeguineae* has been observed to swim among the long spines of diadematid sea urchins, particularly *Echinothrix diadema*, when both the urchin and fish are secluded in crevices or holes in coral mounds. When the urchin is moved outside the hole a short distance some of the cardinal fish venture out and take station among the spines. However, they will not do this if the urchin is moved too far away from the hole or crevice.

Several specimens were found with fish eggs in their stomachs. The presence of these could have resulted from the accidental convulsive swallowing of "incubating" eggs held in the mouth during rotenone poisoning.

Family Priacanthidae

Species: *Priacanthus cruentatus* (big-eye)
Number examined: Eniwetok, 13 specimens
Sex: Males and females
Standard length: 100-235 mm
Digestive tract: Teeth villiform, short; intestine short

Food item	*Percentage of fish containing the item*
Cephalopoda	
Octopus sp.	84
Crustacea	
Pelagic shrimps	53
Shrimp fragments	15
Alpheid shrimps	7
Stomatopod fragments	53
Xanthid crab fragments	15
Portunid crab	7
Crab megalopa	7
Isopods	7
Fish	
Unid. fragments	46
Polychaeta	
Unid. polychaetes	23

This species is locally abundant, particularly on lagoon reefs where there are large crevices or caverns in living coral or coral rubble. Because of its especially large eyes and spelean habitat, most marine biologists have considered this genus to comprise nocturnal feeders. However, the bulk of the food taken by the specimens examined were octopi (*Octopus* sp.) and many had retained the beaks of previously digested ones in their stomachs. It is therefore conceivable that the cryptic habits of both octopi and big-eyes combine to provide these fish a source of food during the daytime. The fact that no stomachs of this species were empty, yet many stomachs of the associated holocentrids (squirrel fish) were empty, leads us to suspect that the big-eye is an active day feeder, but may also forage at night.

Both swimming and bottom-dwelling organisms are taken in amounts which indicate that this species is not restricted in its foraging habits to any particular locality on the reef, but rather is an opportunist. The polychaetes found so abundantly in a few stomachs were a type common in the sandy bottoms adjacent to coral and rubble mounds. Members of this family are abundant carnivores, feeding in caverns, in mid-water and on coral mounds and sandy bottoms.

Family Serranidae

Species: *Epinephelus merra* complex (grouper)
Number examined: Arno, 25; Bikini, 6 specimens: 6 empty
Sex: Males and females
Standard length: 99-360 mm
Digestive tract: Mouth large, outer teeth on jaws villiform, inner rows larger and depressible, short canines at symphysis of each jaw; stomach large, heavy-walled; intestine medium length with a long loop

Food item	*Percentage of fish containing the item*
Fish	
Unid. fragments	28
Gymnothorax margaritophorus	4
Allanetta ovalaua	4
Parupeneus trifasciatus	4
Holocentrus sammara	4
Holocentrid fragments	4
Unid. goby	4
Larval fish	4
Unid. small fish	8
Crustacea	
Crab fragments	24
Portunid fragments	8
Petrolisthes sp.	4
Hippolytid shrimp	4
Shrimp fragments	4
Stomatopod fragments	8
Galathea sp.	4

Essentially, four species are grouped together here which were not segregated taxonomically until after our food analyses had been made and the specimens thrown away. The species involved are *merra, hexagonatus, spilotus,* and *elongatus.* All four have similar appearance and behavior, and occupy essentially the same habitat.

These species are very abundant, demersal, small carnivores which live under ledges near the bottom of coral mounds and rubble. Frequently, they are seen lying motionless on the surface of massive coral formations. They occurred on all reef shallows visited. These groupers forage by lying in wait for prey species to move sufficiently close to them at which time they dash out and seize the victim in their large mouths. No particular selection is made among prey species; they take any small fish or crustaceans which happen by.

Species: *Epinephelus fuscoguttatus* (grouper)
Number examined: Arno, 4; Eniwetok, 4 specimens: 3 empty
Sex: Females
Standard length: 240-360 mm
Digestive tract: Similar to *E. merra*

Food item	*Percentage of fish containing the item*
Fish	
Holocentrus diadema	20
Parupeneus trifasciatus	20
Spratelloides delicatulus	20
Unid. fragments	20
Crustacea	
Thalamita sp.	20
Shrimp fragments	20
Gurry	20

This large solitary grouper is commonly observed lying motionless on the bottom, frequently some distance from protective cover. It also commonly hides under large corals such as *Acropora reticulata* and under rock ledges. This species is one of the commonest large carnivores found on all reefs where the water is six or more feet in depth.

Species: *Epinephelus kohleri* (grouper)
Number examined: Arno, 1; Eniwetok, 1 specimen: 1 empty
Sex: Males
Standard length: 325-370 mm
Digestive tract: Similar to *E. merra*

The one specimen with food contained fish fragments. This species is a large, strongly demersal grouper which usually lies on the bottom near the base of a coral mound in water from 6 to 30 feet in depth. It does not stay away from its refuge place as does *E. fuscoguttatus.* At no place was this species common.

Species: *Epinephelus hexagonatus* (grouper)
Number examined: Bikini, 6 specimens: 2 empty
Sex: Males and females
Standard length: 105-290 mm
Digestive tract: Similar to *E. merra*

Each of the four specimens had taken different species of food items although three of them contained only fish, *Pempheris oualensis,* a juvenile trigger fish, and *Pseudocheilinus* sp. The other specimen had many polychaete fragments in its stomach. This species has the same habits and is found in the same localities on the reefs as is *E. merra,* described earlier.

Species: *Epinephelus macrospilos* (grouper)
Number examined: Eniwetok, 2 specimens: 1 empty
Sex: Female
Standard length: 240-290 mm
Digestive tract: Similar to *E. merra*

The specimen containing food had only fragments of polychaetes. This species, uncommon on most reef areas, grows to about one foot in length, and lurks under expansive coral heads and rock ledges, seldom venturing far from protective cover. Although the specimen examined contained only polychaetes, it is reasonable to expect this species to have food habits similar to other groupers and to take fish, crustaceans, and other invertebrates on occasion.

Species: *Epinephelus spilotus* (grouper)
Number examined: Eniwetok, 12 specimens: 4 empty
Sex: Males and females
Standard length: 170-315 mm
Digestive tract: Similar to *E. merra*

Food item	*Percentage of fish containing the item*
Fish	
Unid. fragments	75
Crustacea	
Crab fragments	25
Shrimp fragments	12
Stenopus hispidus	12
Cephalopoda	
Octopus beaks	12
Sand and pebbles	37

This was a common grouper on all reefs visited. It appears sluggish, often hiding in coral heads or under ledges, but sometimes is seen lying motionless on the bottom well away from protective cover. Its food and feeding habits are similar to other groupers of similar size.

Species: *Variola louti* (grouper)
Number examined: Bikini, 2 specimens: 1 empty
Sex: Female
Standard length: 400 mm
Digestive tract: Similar to *E. merra*

The one specimen with food in its stomach had taken a juvenile surgeon fish, *Naso* sp. This species was uncommon on most reefs visited, preferring lagoon reefs to seaward ones, and was found in deeper water than most other groupers, usually depths in excess of 10 ft. It is solitary, and lives around the deeper coral heads, but frequently is seen hovering in mid-water. It attains a length of about 3 ft, and seems much more agile than other groupers.

Species: *Cephalopholis urodelus* (grouper)
Number examined: Eniwetok, 17; Arno, 3 specimens: 7 empty
Sex: Females and undeveloped
Standard length: 65-190 mm
Digestive tract: Similar to *E. merra*

Food item	*Percentage of fish containing the item*
Fish	
Unid. fragments	42
Crustacea	
Alpheid shrimp fragments	28
Xanthid crab fragments	14
Porcellanid crab fragments	7
Sand grains	7

This species attains about one foot in length, and lurks in holes and crevices of coral heads in all reef areas at depths of 10-12 ft. It is strongly demersal and seldom ventures more than a few feet from its place of refuge.

Species: *Cephalopholis miniatus* (grouper)
Number examined: Eniwetok, 1 specimen: empty
Sex: Undeveloped
Standard length: 280 mm
Digestive tract: Similar to *E. merra*

This is a large, demersal carnivore which lives at considerable depths in the lagoons. It was never observed on the reefs, but several individuals frequented the garbage dump at Eniwetok. Its structure and habits indicate that it is predaceous and probably feeds, like other large groupers, mostly on fish and crustaceans.

Species: *Cephalopholis argus* (grouper)
Number examined: Arno, 3; Bikini, 1; Eniwetok, 8 specimens: 3 empty
Sex: Males and females
Standard length: 130-430 mm
Digestive tract: Similar to *E. merra*

Food item	*Percentage of fish containing the item*
Crustacea	
Shrimp fragments	33
Unid. fragments	11
Fish	
Abudefduf dicki	11
Mullid fragments	11
Unid. fragments	22
Polychaeta	
Unid. polychaetes	11

This medium-sized grouper is common around coral heads from depths of 3-30 ft or more on most reefs. It is a rather active, demersal species which lies in wait for its prey beneath ledges and coral heads. In the Gilbert Islands one specimen of this species examined had taken a shrimp (Randall 1955).

Species: *Anyperodon leucogrammicus* (grouper)
Number examined: Eniwetok, 5 specimens: 2 empty
Sex: Males and females
Standard length: 230-350 mm
Digestive tract: Similar to *E. merra*

One of the three specimens with food had unidentified fish fragments in its stomach; another had a goat fish and the third had only the foraminiferan, *Calcarina* sp., along with sand grains of the same size, caught in the folds of its stomach mucosa. This species is uncommon, but present in lagoon reef areas and seaward reefs where the water is not turbulent. It secludes itself under corals almost all of the time, and is rarely observed by the skin-diver. Doubtless it lies motionless under corals watching for fish or invertebrates to pass by closely enough so that it may lunge out to seize them.

Species: *Plectropomus truncatus* (grouper)
Number examined: Eniwetok, 3 specimens: 2 empty
Sex: Undeveloped
Standard length: 295-600 mm
Digestive tract: Similar to *E. merra*, but with enlarged canines.

The one specimen containing food had a squirrel fish, *Holocentrus* sp., in its stomach. This species is common on reefs having an abundance of living coral from 4-20 ft in depth. It is more active and less demersal than other groupers, characteristically hovering in mid-water. It is shy and difficult for a swimmer to approach. It especially hovers in surge channels of the seaward reefs, or just over the reef front 6-20 ft below the surface. Although only one of the three specimens examined contained a fish as food, it is rather certain that fish are the principal food items taken.

Family Summary

Although all the members of this family are voracious carnivores ubiquitous on Marshallese coral reefs, there are great differences in habits between the smaller and larger species, and among the larger species certain pertinent differences occur. Most of the smaller species are demersal and conceal themselves in crevices or holes in corals, or under ledges and rocks in coral rubble. Their characteristic habit is to lie motionless on the bottom, mostly concealed by the coral except for the head always directed outward, where they lie in wait for unwary small fish or invertebrates to come within their reach. A rapid lunge of a few inches to a few feet is made to catch their prey. Some of the larger species can always be found lying motionless on sandy or rubble bottoms just a few feet from coral mounds. They appear to pay little attention to swimmers at the surface, but little by little they move further outward to deep water.

Certain of the larger species, notably *V. louti*, characteristically hover in mid-water near the coral caverns in which they seclude themselves. Still others, *Plectropomus truncatus* and *P. leopardus*, hover in mid-water over open areas in surge channels, just over the seaward reef edge, or near coral mounds and patches in deeper water on the lagoon reefs.

Groupers are not notoriously rapid swimmers; hence, even those larger forms which hover in open water, or those which are demersal and lie motionless on the bottom, probably subsist to a great extent on crustaceans and coral-dwelling fish which venture too closely to them. It is doubtful that they could catch other mid-water fishes.

Family Pseudochromidae

Species: *Plesiops melas*
Number examined: Arno, 15; Eniwetok, 1 specimen: 1 empty
Sex: Males and females
Standard length: 36-58 mm
Digestive tract: Mouth large, teeth in villiform bands on both jaws; intestine short.

Food item	*Percentage of fish containing the item*
Crustacea	
Crab fragments	33
Hermit crab fragments	13
Xanthid crab fragments	6
Shrimp fragments	6
Alpheus sp. fragments	6
Fish	
Unid. fragments	20
Eviota sp.	13
Gastropoda	
Unid. gastropod fragments	20
Sand	6

This species, common at Arno, was rather uncommon at Eniwetok. It lives on the interisland reef and seaward reefs where the wave action is rather strong. The species is demersal and hides in and under living coral. It characteristically remains motionless while lying in wait for its prey which comprises members of the benthonic fauna.

Species: *Plesiops nigricans*
Number examined: Arno, 6 specimens
Sex: Males and females
Standard length: 74-119 mm
Digestive tract: Similar to *P. melas*

Food item	*Percentage of fish containing the item*
Crustacea	
Crab fragments	50
Portunus longispinosus bidens	17
Xanthid crab fragments	17
Coenobita sp.	17
Hermit crab fragments	17
Galathea sp.	17
Copepods	17
Fish	
Unid. fragments	34
Abudefduf glaucus	17
Apogon novemfasciatus	17

This species was especially common at Arno Atoll on the seaward reef shallows. It is mainly an intertidal species and is commonly found stranded in small tide pools containing loose boulders, or even under rocks completely exposed at low tide. It is a voracious carnivore which apparently darts out from its hiding place to seize its prey which consists of benthonic intertidal crustaceans and small fish associated with corals in shallow water, or tide pool inhabitants.

Species: *Pseudogramma polyacantha*
Number examined: Arno, 13; Bikini, 3 specimens: 5 empty
Sex: Males and females
Standard length: 28-65 mm
Digestive tract: Similar to *P. melas*

Food item	*Percentage of fish containing the item*
Crustacea	
Shrimp fragments	54
Crab fragments	27
Xanthid crab fragments	9
Fish	
Unid. fragments	9

This species was uncommon at Eniwetok, but rather abundant at Arno Atoll, on both the lagoon and seaward reef shallows near living coral. It habitually hides in and under living coral and has a demersal nature. Like others of this family it lies in wait for prey to come sufficiently close to capture, and thus feeds mostly on benthonic crustaceans and small fish associated with living coral.

Species: *Pseudochromis tapeinosoma*
Number examined: Arno, 2 specimens
Sex: Males
Standard length: 29-37 mm
Digestive tract: As in *P. melas*, except that jaws contain teeth in villiform bands and strong canines

Both specimens examined had taken small crustaceans, and contained crab fragments, isopods, and copepods. This very small species, uncommon at Eniwetok, was common both at Bikini and at Arno in living coral both on the lagoon and seaward reefs. It is demersal, and doubtless feeds by lying in wait for small crustaceans to come close to it.

Family Summary

All species of this family live under ledges and rocks and in interstices of living corals, rather similar in habits to the demersal groupers. Only *P. nigricans* is found in the intertidal zone where it is a characteristic carnivore in tide pools. All are voracious carnivores, although small in size, feeding predominantly on crustaceans, but taking any prey the proper size. Their characteristic feeding method is to lie in wait for prey species to come near enough for capture, which is then accomplished by a rapid lunge.

Family Pempheridae

Species: *Pempheris oualensis* (sweeper)
Number examined: Bikini, 11; Eniwetok, 5 specimens: 1 empty
Sex: Males and females
Standard length: 75-180 mm
Digestive tract: Mouth moderate in size, teeth in villiform bands on the jaws; intestine short

Food item	*Percentage of fish containing the item*
Crustacea	
Shrimp fragments	26
Alpheid shrimps	6
Xanthid crab fragments	26
Trapezia sp.	20
Crab megalopa	20
Stomatopod fragments	13
Odontodactylus sp.	6
Copepods	6
Polychaeta	
Unid. pelagic polychaetes	20
Polynoid polychaetes	6
Cephalopoda	
Octopus cyanea	6
Fish	
Juvenile wrasses	6

Sweepers are abundant locally at all three atolls, most commonly in seaward reef surge channels or under overhanging reef ledges at the seaward edge where they are subjected to severe wave action. Frequently large numbers school at the head of surge channels. They also occur commonly on the lagoon reef around large coral mounds in water 10-20 ft in depth. They appear to be voracious carnivores usually having the stomachs crammed with food, mainly crustaceans.

Family Lutjanidae

Species: *Lutjanus monostigmus* (snapper)
Number examined: Eniwetok, 3 specimens: 2 empty
Sex: Female
Standard length: 345-365 mm
Digestive tract: Mouth large, canines well developed on sides of jaws; stomach thick-walled; intestine short, one loop

The single specimen containing food had eaten several goat fish (Mullidae). This species does not wander about, but remains in small schools in the deeper waters of the lagoon reef. Frequently, it may be seen in large caverns in the coral mounds. The young swim in larger schools on the seaward reef shallows and interisland reef shallows.

Species: *Lutjanus bohar* (snapper)
Number examined: Bikini, 2 specimens: 1 empty
Sex: Males
Standard length: 470-550 mm
Digestive tract: Similar to *L. monostigmus*

The one specimen containing food had unidentified fish fragments in its stomach. This large snapper was never seen in the shallow reef areas, but was seen occasionally in deeper water down the lagoon reef slope or off the seaward reef edge. It is a hovering, mid-water carnivore.

Species: *Lutjanus vitta* (snapper)
Numbers examined: Arno, 2; Eniwetok, 24 specimens: 8 empty
Sex: Males and females
Standard length: 161-255 mm
Digestive tract: As in *L. monostigmus*

Food item	*Percentage of fish containing the item*
Crustacea	
Shrimp fragments	38
Portunid crabs	27
Crab fragments	27
Stomatopod fragments	5
Fish	
Unid. fragments	11
Spratelloides delicatulus	11
Polychaeta	
Unid. fragments	5
Chordata	
Ptychodera sp.	5

This snapper is very abundant in the Marshall Islands, and was observed commonly in schools, comprised, frequently, of both *L. vitta* and *L. gibbus*, along rocky ledges bordering sandy patches. It was also observed frequently in large holes 6-8 ft deep in the interisland reefs at Eniwetok. Apparently, it feeds from the surface to the bottom, as the food items range from surface swimming round herring, *S. delicatulus*, to fossorial balanoglossids, *Ptychodera* sp.

Species: *Lutjanus vaigiensis* (snapper)
Number examined: Arno, 6 specimens
Sex: Undeveloped
Standard length: 33-58 mm
Digestive tract: Similar to *L. monostigmus*

Food item	*Percentage of fish containing the item*
Crustacea	
Crab fragments	50
Amphipods	33
Shrimp fragments	17
Stomatopod fragments	17
Fish	
Unid. fragments	50

The specimens examined were all juveniles taken from a large school on the lagoon reef at Arno in water about 5 ft deep. At this age they apparently feed mostly on the benthonic fauna in shallow water. The adults reach about 18 inches in length, and probably have different habits than those indicated here for the juveniles. However, Randall (1955) reported on the food of two larger *vaigiensis* from the Gilbert Islands and listed a small crab for one and a small holothurian for the other, both benthonic forms.

Species: *Lutjanus gibbus* (snapper)
Number examined: Arno, 1; Eniwetok, 32 specimens: 10 empty
Sex: Males and females
Standard length: 175-260 mm
Digestive tract: Similar to *L. monostigmus*

Food item	*Percentage of fish containing the item*
Crustacea	
Xanthid crab fragments	60
Portunid crab fragments	17
Kraussia rugulosus	8
Parthenopid crabs	4
Hermit crabs (*Calcinus* sp.)	4
Alpheid shrimp	4
Alpheus ventrosus	4
Shrimp fragments	4
Amphineura	
Solenogastrid (*Neomenius* sp.)	13
Cephalopoda	
Octopus sp.	4
Gastropoda	
Natica sp.	4
Chordata	
Ptychodera sp.	4
Echinodermata	
Small unid. holothurians	4
Polychaeta	
Unid. polychaetes	4
Sipunculoidea	
Unid. fragments	4
Fish	
Apogon erythrinus	4

This snapper is one of the most abundant in the Marshall Islands. It is seen commonly on all reefs, particularly in the interisland reefs where coral growth is luxuriant and the water is at least 6-8 ft deep. At Arno huge schools moved back and forth just beyond the seaward reef edge. It feeds just about everywhere on the reefs, taking species commonly associated with living, branching corals, and benthonic fauna characteristic of sandy bottoms, some of which are fossorial species. It depends primarily upon crustaceans, the bulk of which are sandy-bottom dwellers.

Species: *Scolopsis cancellatus* (snapper)
Number examined: Arno, 3 specimens: 1 empty
Sex: Males and females
Standard length: 40-137 mm.
Digestive tract: Similar to *L. monostigmus*

One specimen contained crab fragments and the other had only gurry. This species lives near branching corals, especially at the protected seaward reef edge and the lagoon reef edge. Because of its structure and habits it is probably predacious on crustaceans and small fish.

Species: *Gymnocranius griseus* (snapper)
Number examined: Arno, 1; Eniwetok, 1 specimen
Sex: Female
Standard length: 298-375 mm
Digestive tract: Mouth moderate in size, teeth short, canines near symphyses of jaws, rounded and molariform on sides of jaws; stomach heavy-walled; intestine moderately short with slight looping

In the two specimens examined the following food items were found: Crustacea—*Thalamita* sp., Xanthid crab fragments; Echinodermata—*Holothuria* sp. (entire specimen), *Maretia* sp. (heart urchin); Pelecypoda—Unid. clam.

This species has rather different food habits than other lutjanids examined, as would be expected from its highly modified dentition. It is strictly a feeder on the benthonic fauna, and more particularly on the fossorial types, many of which are hard shelled and must be crushed before being digested. It has been observed in the process of foraging on sandy bottoms where it "blows" the sand away from buried prey. *G. griseus* is a rather slow-swimming "solemn" appearing fish. It is often seen in groups of two or three individuals hovering around large coral mounds adjacent to open sandy areas. They slowly circle these coral mounds keeping an eye on skin divers.

Species: *Lethrinus microdon* (snapper)
Number examined: Eniwetok, 2 specimens
Sex: Male and female
Standard length: 270-340 mm
Digestive tract: Similar to *L. monostigmus*

The two specimens examined had eaten the following: Crustacea—Maiid crab; Portunid crab; Crab fragments; Fish—Unid. fragments.

This species is solitary and occurs only in the deeper water over the lagoon reef slope. None were seen in water shallower than 15 ft. According to the food items eaten, the species must swim close to the bottom where it feeds on benthonic crustaceans primarily. Al=Hussaini (1947) reports that two species of this genus in the Red Sea also prefer benthonic crustaceans, but take a wide variety of prey, including echinoderms and molluscs.

Species: *Aprion virescens* (streaker)
Number examined: Eniwetok, 3 specimens: all empty
Sex: Males and females

Standard length: 540-760 mm
Digestive tract: Mouth very large, teeth strongly developed, heavy canines; intestine moderately short

The specimens examined had been eating garbage, but this species is a large, solitary, voracious carnivore which hovers in mid-water over the lagoon reef slope from 10-40 ft in depth. It will cruise quite slowly up to the shallows in search of prey, but when disturbed it moves back into deeper water, where it swims along the bottom. At no time have we seen this fish feeding, except during rotenone poisoning stations, but there is no doubt about its niche being that of a voracious, roving carnivore on the lagoon reefs.

Species: *Gnathodentex aureolineatus*
Number examined: Bikini, 4 specimens
Sex: Males and females
Standard length: 160-180 mm
Digestive tract: Both jaws with outer row of conical canines, three pairs of which are enlarged at front of jaws; intestine moderately short

Food item	*Percentage of fish containing the item*
Crustacea	
Xanthid crabs	100
Gastropoda	
Cerithium sp.	75
Polychaeta	
Unid. fragments	25
Fish	
Stenatherina temmincki	25
Unid. fragments	25

This species frequents the relatively deep water over the lagoon reefs and the surge channels along the seaward reef margin. It is apparently a solitary carnivore which takes both food at the surface or in mid-water (silversides) and benthonic fauna (xanthid crabs, polychaetes, and gastropods).

Family Summary

Snappers are all carnivorous fish, with one possible exception, *Macolor niger*, which will be discussed below. They vary in size from small fish a few inches in length to some of the largest of the reef-dwelling species, exceeding 3 ft. Several species school (*Lutjanus kasmira, gibbus, vitta*), but most are solitary or occur as loosely organized aggregations. The largest species, i.e., *L. bohar*, and *A. virescens*, are solitary. All have large mouths and strong dentition. By and large they seem to be predominantly benthonic feeders and swim just above the bottom. A few, of which *A. virescens* is a good example, are mid-water forms. At least three species, *L. vitta, L. gibbus,* and *Gymnocranius griseus*, take fossorial forms, with the latter species having developed the proper dentition and habits to feed almost exclusively on hard shelled clams, heart urchins, and gastropods. Except for *G. griseus* very little specificity is shown in types of prey taken; most capture any type of fish or invertebrate which they contact and can handle. Randall (1955) examined a few lutjanids in the Gilbert Islands and found similar feeding habits to those described here.

One species, *Macolor niger*, was taken by hook and line from the Eniwetok pier, so was not included in the food study. However, its great divergence in food habits and structural features from the usual snapper make it worthwhile to mention here. This species has the gill rakers modified for sieving plankton and they project well forward into the buccal cavity. However, the fact that it was caught on a baited hook indicates that it is by no means restricted to a planktonic diet. Species of the genus *Caesio* are full-fledged plankton feeders, but none were collected for our study. Randall (1955) reports the food of *C. xanthonotus* in the Gilbert Islands to consist of pelagic copepods, mollusc larvae, shrimp nauplii, and fish eggs.

Thus, the family Lutjanidae comprises a heterogeneous group of fishes as regards their food and feeding habits and associated structural modifications. This heterogeneity is reflected in the many taxonomic changes made by successive authors in evaluating the parameters of this family.

Family Leiognathidae

Species: *Gerres argyreus* (silver perch)
Number examined: Arno, 2 specimens
Sex: Female
Standard length: 133-186 mm
Digestive tract: Rather long, highly protrusible snout, small teeth in villiform bands on both jaws; stomach thin-walled; intestine long, coiled.

The following food items were found in the two specimens examined: Crustacea—Isopods, Ostracods; Polychaeta—Unid. polychaetes; Foraminifera; Algae—Algal scrapings, little sand; Algal filaments, little sand.

Silver perch are solitary individuals distributed usually over sandy bottoms in quiet lagoon reef waters from 6-30 ft. deep. They work busily at stirring up the surface layers of the bottom with their protrusible snouts, taking anything edible. They are clearly omnivorous in habits, a fact reflected by the long, coiled intestine and thin-walled stomach. Al=Hussaini (1947) found *G. oyena* in the Red Sea to prefer polychaetes, but to take also such items as small crustaceans, fish, and other organisms.

Family Sparidae

Species: ***Monotaxis grandoculis***
Number examined: Arno, 3; Eniwetok, 5 specimens: 1 empty
Sex: Males and females
Standard length: 195-250 mm
Digestive tract: Mouth moderately large, both jaws with a single row of molar teeth, the posterior few very broad and heavy, strong canines at front of both jaws; stomach heavy-walled; intestine of medium length.

Food item	*Percentage of fish containing the item*
Gastropoda	
Crushed *Atys* sp. and *Cerithium* sp.	100
Pelecypoda	
Crushed sand-dwelling clams, few whole	71
Crustacea	
Crushed crab fragments	42
Portunid crabs	28
Parthenopid crabs	14
Hermit crabs (crushed gastropod shells)	28
Echinodermata	
Small spatangids, crushed	14
Polychaeta	
Unid. polychaetes	14

This species is always found alongside coral mounds, swimming slowly or hovering over sandy patches. It is most often solitary, but does form loose aggregations of two or three individuals at times. Its food habits and dental structure designate it as a feeder on fossorial forms, taking hard-bodied species which are crushed with the massive grinding-, crushing-type molariform teeth. When feeding this fish virtually stands on its head and ''blows'' away the sand surrounding its prey. Randall (1955) found specimens in the Gilbert Islands to feed as reported here.

This genus is frequently included with the family Lutjanidae (Schultz *et al.* 1953). However, we believe that it is sufficiently distinct, structurally and behavioristically, to merit its taxonomic segregation.

Family Mullidae

Species: *Mulloidichthys samoensis* (goatfish)
Number examined: Arno, 19; Bikini, 7; Eniwetok, 8 specimens: 11 empty
Sex: Males and females
Standard length: 81-250 mm
Digestive tract: Chin with barbels, mouth medium, teeth minute; stomach V-shaped; intestine medium-long

Food item	*Percentage of fish containing the item*
Fish	
Gurry	42
Unid. fragments	28
Polychaeta	
Unid. polychaetes	14
Sabellids	4
Crustacea	
Shrimp fragments	14
Crab fragments	9
Hermit crab fragments	9
Cyclopoid copepods	9
Pelecypoda	
Semelangulus sp.	14
Gastropoda	
Crushed gastropods	9
Echinodermata	
Spatangid fragments	9
Chordata	
Ptychodera sp.	4
Sand, including foraminiferans	14

This species was found in large schools of 25-100 individuals swimming over and probing sandy bottoms with their barbels. They are especially abundant on shallow lagoon shores and on seaward reef flats when the tide is high. As its food items indicate, it consumes fossorial as well as surface benthonic fauna. At Eniwetok the specimens examined had been feeding heavily on the small clam, *Semelangulus* sp.

Species: *Parupeneus trifasciatus* (goatfish)
Number examined: Arno, 27 specimens: 3 empty
Sex: Males and undeveloped
Standard length: 46-150 mm
Digestive tract: Similar to *M. samoensis*

Food item	*Percentage of fish containing the item*
Crustacea	
Xanthid crab fragments	17
Maiid crab fragments	12
Shrimp fragments	33
Unid. shrimps	17
Alpheus sp.	17
Cyclopoid copepods	12
Calanoid copepods	8
Copepod metanauplii	4
Ostracods	8
Tanaid isopods	8
Amphipods	4
Galathea sp.	4
Fish	
Unid. fragments	20
Gastropods	
Oliva sp.	12
Polychaeta	
Unid. polychaetes	4
Foraminifera	
Calcarina sp.	8

P. trifasciatus is a small goatfish which occurs in groups of two or three on virtually all reefs from 3-10 ft deep. Frequently it is seen probing the sand with its barbels around the base of coral heads. It forages in typical goatfish fashion, but takes mostly smaller crustaceans, other invertebrates, and small benthonic fish. In the Gilbert Islands, Randall (1955) reported this fish to have consumed amphipods, copepods, and other small crustaceans.

Species: *Parupeneus barberinus* (goatfish)
Number examined: Arno, 9; Eniwetok, 3 specimens
Sex: Males
Standard length: 60-390 mm
Digestive tract: Similar to *M. samoensis*

Food item	*Percentage of fish containing the item*
Polychaeta	
Unid. polychaetes	58
Crustacea	
Shrimp fragments	41
Ostracods	25
Isopods	25
Thalamita sp.	17
Tetralia globerrima	8
Xanthid crabs	8
Amphipods	8
Copepods	8
Nebalaceans	8
Foraminifera	
Calcarina sp.	8
Sand grains	8

This species is common in groups of two or three over sandy-bottom areas on all reefs in water 2-30 ft deep. It reaches a large size. Its foraging habits are similar to other goatfish, consequently, polychaetes and benthonic crustaceans predominate in its diet.

Species: *Parupeneus cyclostomus* (goatfish)
Number examined: Bikini, 1; Eniwetok, 5 specimens: 2 empty
Sex: Males and females
Standard length: 130-285 mm
Digestive tract: Similar to *M. samoensis*

Food item	*Percentage of fish containing the item*
Crustacea	
Thalamita sp.	75
Xanthid crabs	25
Odontodactylus sp.	50
Shrimp larvae	25
Alpheid shrimps	25
Amphipods	25
Galathea sp.	25
Fish	
Unid. fragments	50
Wrasse, small	25
Calymmichthys goramensis	25
Eviota sp.	25
Gnatholepis anjerensis	25

This comparatively large goatfish is usually found solitary, although loose aggregations of two or three are commonly seen on all reefs with open sandy areas in water from 1-20 ft deep. It probes the bottom actively, now and then stirring up the sand to capture crustaceans hidden there. It is an active feeder on small, benthonic fish species also. Frequently rather extensive bottom areas are left "rooted" up as the result of the foraging habits of this species.

Species: *Upeneus arge* (goatfish)
Number examined: Eniwetok, 2 specimens
Sex: Male and female
Standard length: 260-270 mm
Digestive tract: Similar to *M. samoensis*

The two specimens contained the following food items in their stomachs: Crustacea—*Thalamita* sp., *Callappa* sp., *Callianassa* sp., Unid. shrimp. This rather large species schools in groups numbering five to about 50 individuals, and frequents sandy-bottom areas on the lagoon reef in water 4-15 ft deep and on the seaward reef flat. It does not probe the sand with its barbels as do other goatfish, but rather seeks out those benthonic crustaceans living exposed on the sandy bottoms. Perhaps because it does not probe, it seems much swifter than other goatfish. Suyehiro (1942) reports that *U. bensasi* feeds rather similarly in Japan, having found alpheid shrimps, amphipods, crawling shrimps (*Crago* sp.) and sand worms (*Nereis* sp.) in their stomachs.

Family Summary

Goatfish are small to medium-sized fish, some solitary, others schooling, which frequent the sandy bottom areas of all reefs and the seaward reef flats when sufficiently covered by the rising tide. Except for the rapidly swimming *U. arge,* most busily probe the sand, moving very slowly, giving it a thorough searching for prey. Both surface benthonic forms and fossorial species are captured. In general they avoid hard-bodied fossorial forms such as clams and echinoderms because they have no crushing dentition. The teeth are mostly small and weak, restricting them to crustaceans and soft-bodied invertebrates.

Family Cirrhitidae

Species: *Amblycirrhitus arcatus* (hawkfish)
Number examined: Arno, 18; Bikini, 1; Eniwetok, 1 specimen: 3 empty
Sex: Males and females
Standard length: 46-72 mm
Digestive tract: Mouth large, teeth not strongly developed; intestine short straight.

Food item	*Percentage of fish containing the item*
Fish	
Unid. fragments	47
Stenatherina temmincki	5
Parapercid	5
Crustacea	
Galathea sp.	17
Xanthid crab fragments	11
Thalamita sp.	5
Maiid crab fragments	5
Trapezia sp.	5
Hippolytid shrimps	5
Leander sp.	5
Alpheus sp.	5
Isopods	5

This solitary species is ubiquitous in reef areas containing large, living coral heads. It habitually lies motionless on the upper surface of living coral heads waiting for crustaceans and small fishes to come within range of its rapid thrust to capture them. It does not move much even if disturbed. Its food items are those very closely associated with living coral, hence it need not venture far away from its home base.

Species: *Paracirrhites forsteri* (hawfish)
Number examined: Arno, 7; Bikini, 1 specimen
Sex: Females
Standard length: 50-137 mm
Digestive tract: Similar to *A. arcatus*

Food item	*Percentage of fish containing the item*
Fish	
Unid. fragments	62
Wrasses, young	25
Chromis caeruleus	12
Istiblennius sp.	12
Fish eggs	12

This species has very similar habits to those of *A. arcatus,* and occupies the same general areas of the reef. Its food habits seem to run to fish rather more than to crustacea as contrasted with *A. arcatus,* but this may be the result of the larger size of *P. forsteri.* Randall (1955) reports that one of this species examined in the Gilbert Islands contained a shrimp.

Species: *Cirrhitichthys aprinus* (hawkfish)
Number examined: Arno, 3 specimens
Sex: Females
Standard length: 42-48 mm
Digestive tract: Similar to *A. arcatus*

The following food items were found in the stomachs of the three fish examined: Crustacea—Isopods, Amphipods, Crab fragments; Fish—Unid. fragments, Fish eggs; Polychaeta. This small hawkfish remains under ledges and in branching coral near the outer reef edges on both lagoon and seaward reefs, and does not lie in exposed areas as do the two species previously mentioned. It has not been observed in the act of feeding, but apparently it takes any small forms which approach it closely enough for capture.

Species: *Cirrhitus pinnulatus* (hawkfish)
Number examined: Bikini, 1 specimen
Sex: Female
Standard length: 140 mm
Digestive tract: Similar to *A. arcatus*

The one specimen examined contained a small coral crab, *Trapezia* sp. This species resides commonly at the outer edge of the seaward reef where it lies in holes in living coral and feeds in the interestices. Similar habits for this species were mentioned by Randall (1955) for a specimen from the Gilbert Islands.

Family Summary

Hawkfish are small, solitary, demersal carnivores which lie in wait for their prey which consists mostly of crustaceans and small fish closely associated with living corals. The larger members of the family usually lie motionless on the tops and sloping sides of living coral heads, rather than partially concealed as do the small groupers. Those that lie in exposed situations are brilliantly colored and very easily seen on the coral. None are protectively or obliteratively colored, but rather appear to possess warning colors. They are sluggish when molested, moving only a few inches or a few feet. *C. pinnulatus,* however, is actually camouflaged comparable to the patterns exhibited by a scorpaenid.

Family Siganidae

Species: *Siganus rostratus* (rabbitfish)
Number examined: Arno, 2; Bikini, 3; Eniwetok, 10 specimens
Sex: Males and females
Standard length: 167-310 mm
Digestive tract: Mouth small, numerous small, conical teeth in each jaw, pharyngeal teeth well developed; stomach rather thick-walled; intestine broad, extremely long, coiled, and thick-walled

Food item	*Percentage of fish containing the item*
Algae	
Scraped algal filaments with calcareous powder	60
Fronds bitten off, no sand	40
Foraminifera	
Calcarina sp. (probably taken with scraped algae)	20

Rabbitfish are abundant on Marshallese reefs, particularly on interisland reefs and seaward reef flats during high tide, where they occur in dense schools of from 20-500 individuals. They are busy feeders, browsing head down on algal covered rocky bottoms, moving slowly along. Little attention is paid to skin-divers in the vicinity of these schools. The species is herbivorous, and may be classed as a typical browser. It, like a number of other naturally herbivorous species (Family Acanthuridae), becomes an habitué of garbage dumps where it consumes waste meat scraps. This indicates that it is not an obligatory herbivore and that both its feeding and digestive apparatus can convert to a fleshy diet on occasion.

Suyehiro (1942), in mentioning the earlier studies of Uchida on this genus, stated that this worker had found the smaller individuals (140 mm) feeding chiefly on copepods and those from 180 to 200 mm on diatoms and seaweeds, i.e., as they grew older they turned more and more to an herbivorous diet. Sueyhiro, in his own investigation, failed to find any evidence for ascribing a carnivorous diet to the young and classed them as herbivorous, even though some animal food was admixed with the prodigious quantities of algae eaten. Our results agree perfectly with his findings.

Family Kyphosidae

Species: *Kyphosus cinerascens* (pilot fish, rudder fish)
Number examined: Arno, 1; Eniwetok, 3 specimens: 1 contained garbage only
Sex: Males and females
Standard length: 230-345 mm
Digestive tract: Mouth small, protrusible, both jaws with a uniserial outer row of obtusely lanceolate incisors, with minute villiform teeth behind; stomach a two part gizzard; intestine very long, coiled

The specimens examined contained fronds and filaments of algae bitten off and scraped, but with no sand or calcareous powder.

This kyphosid occurred in small schools, usually swimming rapidly in mid-water or near the surface on both lagoon and seaward reefs at depths of 6-20 ft. It was especially abundant just beyond the reef edge of the seaward reefs. It is a strictly herbivorous species which may be classed as a browser.

Family Chaetodontidae

Species: *Chaetodon lunula* (butterfly fish)
Number examined: Eniwetok, 1 specimen
Sex: Female
Standard length: 135 mm
Digestive tract: Mouth very small, snout somewhat produced, teeth long, slender, straight, bent at tip where they taper to a point; stomach Y-shaped, thick-walled; intestine long, coiled

The specimen examined contained many browsed tips of coral polyps. This chaetodontid was frequently observed swimming close to isolated coral heads surrounded by patches of sand. The adults were seen most commonly in the lagoon to depths of 10 feet, while the young were most abundant on the seaward reef shallows. It is a rather shy species, always turning the edge of the body to a skin-diver, so as to make it virtually impossible to spear. In confinement this species will take occasional scraps of meat, and frequently browses on algae growing on the walls of the tank.

Species: *Chaetodon citrinellus* (butterfly fish)
Number examined: Arno, 4; Bikini, 2; Eniwetok, 10 specimens
Sex: Males and females
Standard length: 39-95 mm
Digestive tract: Similar to *C. lunula*

Food item	*Percentage of fish containing the item*
Coelenterata	
Coral polyps, no skeletal material	61
Coral polyps, some skeletal material	33
Algae	
Algal scrapings, no calcareous powder	11
Algal scrapings, with calcareous powder	5
Polychaeta	
Unid. polychaetes	5

This butterfly fish is abundant in and around coral heads at depths of 2-20 ft in the lagoon, interisland reefs, and the seaward reef. Frequently it can be seen browsing on the surface of live coral heads, particularly *Acropora* and *Porites*, where it nibbles off the small coral polyps extending from the corallites. Living coral heads placed in confinement with this chaetodontid were browsed in the same manner while under careful observation by us. The species is not restricted to a diet of polyps, however, as it is also capable of scraping fine filaments of algae off rocks and dead bases of coral heads, as well as taking polychaetes from interstices of living coral heads.

Species: *Chaetodon ephippium* (butterfly fish)
Number examined: Arno, 4; Eniwetok 6 specimens
Sex: Males and females
Standard length: 123-160 mm
Digestive tract: Similar to *C. lunula*

Food item	*Percentage of fish containing the item*
Coelenterata	
Coral polyps, with skeletal particles	60
Algae	
Fine filaments, no calcareous material	50
Crustacea	
Shrimp fragments	10
Polychaeta	
Unid. polychaetes	10

This species is very common around living coral on all reefs in water 2-25 ft deep. Unlike most butterfly fish, it is also commonly seen in sandy regions containing but few coral heads. Its feeding habits are similar to the chaetodontids described above.

Species: *Chaetodon vagabundus* (butterfly fish)
Number examined: Arno, 4 specimens
Sex: Males
Standard length: 58-85 mm
Digestive tract: Similar to *C. lunula*

Food item	*Percentage of fish containing the item*
Coelenterata	
Coral polyps, with skeletal particles	75
Algae	
Fine scrapings, with calcareous powder	25
Filaments, without calcareous powder	25

This species was common only at Arno Atoll, and apparently does not occur at all, or is extremely rare, in the northern Marshall Islands. It swims about living coral on both the lagoon, and seaward reefs, and doubtless does likewise on the interisland reefs. Its food and feeding habits are similar to the chaetodontids described above.

Species: *Chaetodon reticulatus* (butterfly fish)
Number examined: Bikini, 1 specimen
Sex: Male
Standard length: 110 mm
Digestive tract: Similar to *C. lunula*, except that the teeth are very fine, numerous, flexible and brush-like

The one specimen examined contained only fine filamentous algae. This species is common on the seaward reef flats, particularly on the outer half, and in quiet waters of the lagoon rich in living coral. It habitually remains in hiding in crevices and holes in the coral. It has been observed to graze on the fine algal filaments which cover the seaward reef shallows, and apparently does not take coral polyps, at least to any great extent.

Species: *Chaetodon auriga* (butterfly fish)
Number examined: Arno, 15; Bikini, 1; Eniwetok, 13 specimens: 1 empty
Sex: Males and females
Standard length: 43-165 mm
Digestive tract: Similar to *C. lunula*

Food item	*Percentage of fish containing the item*
Polychaeta	
Unid. polychaetes	46
Coelenterata	
Coral polyps, no skeletal material	28

Algae	
Fine filaments, no calcareous powder	25
Fine filaments, with calcareous powder	3
Crustacea	
Shrimp fragments	10
Alpheus sp.	3
Tetralia sp.	3
Ostracods	3
Gastropoda	
Egg masses	7
Vermetid fragment	3
Nemertinea	10
Foraminifera	
Calcarina sp.	3

This is a common butterfly fish on all reefs visited in water 2-25 ft in depth. It frequently is seen swimming over sandy areas near coral rubble, rather far removed from beds of living coral. Its food is more heterogeneous than other chaetodontids, although it is still classed as omnivorous. The predilection for polychaete worms noted for this species is not shared to the same extent by other members of the family. In confinement with living coral, it busily nibbles off the polyps. Its feeding habits are extremely facultative, which probably accounts for its food forays over sandy areas and in coral rubble not closely adjacent to living corals.

Species: *Megaprotodon strigangulus* (butterfly fish)
Number examined: Eniwetok, 11 specimens: 2 empty
Sex: Males and females
Standard length: 60-110 mm
Digestive tract: Similar to *C. lunula*, except that the teeth are massed toward front of jaws and protrude

All specimens with food in their stomachs contained only coral polyps with no skeletal material admixed. This species is very common on all reefs visited where living coral is abundant. It stays very close to living corals, never venturing more than a few feet away from cover. It is the only chaetodontid which seems to feed exclusively on coral polyps in nature, and its dentition is especially suited to this feeding habit. However, in confinement it will graze on encrusting algal filaments and take meat scraps.

Species: *Centropyge flavissimus* (angel fish)
Number examined: Arno, 8; Bikini, 2; Eniwetok, 2 specimens
Sex: Male and female
Standard length: 45-75 mm
Digestive tract: Snout not produced, mouth small, teeth setiform, long, flattened, tricuspid, the middle lobe much larger than the lateral lobes; intestine very long, coiled, rectum huge

These specimens had taken algae exclusively, with 88% of them biting off algal fronds which had no calcareous powder admixed, and 12% had scraped fine filaments of algae in which some calcareous powder was mixed. This angel fish is common around living coral, usually hiding in crevices or holes, on all reefs in quiet water 4-15 ft deep. It is entirely herbivorous, mostly a browser, but occasionally a grazer.

Family Summary

The chaetodontids are brilliantly colored, laterally highly compressed, deep-bodied fish as typical of coral reefs as the corals themselves. They occur singly or in pairs on both lagoon, seaward, and interisland reefs wherever coral growth is luxuriant.

Considerable heterogeneity is evident as regards the food and feeding habits of the several members of this family examined. Some appear to be rather strict herbivores, grazing or browsing short algal filaments on reef rock or on the dead bases of coral heads (*C. reticulatus* and *Centropyge flavissimus*). Others seem to have a strong predilection for browsing and grazing off polyps of coral as well as algal filaments, and thus are omnivores (*C. citrinellus, C. ephippium, C. vagabundus*). Yet others are strictly browsers on coral polyps, and thus are carnivores (*C. lunula, Megaprotodon strigangulus*). Only one, *C. auriga*, is an habitual non-selective omnivore, although polychaetes comprise the bulk of its diet.

It is of interest to note, from the standpoint of feeding methods and related structural modification of the dentition, that the less specific omnivorous species which take coral polyps as part of their diet, along with algae, always contain a considerable amount of calcareous skeletal particles admixed with the food; whereas, those which are selective and consume only coral polyps do not have this admixture of calcareous skeletal material. These observations suggest that the latter species have attained a higher degree of adeptness in nibbling off the polyps. It is apparent that the omnivorous species must scrape the fine algal filaments off rocks and dead coral bases, so when taking coral polyps they probably also scrape the surface, rather than neatly biting off the polyp without touching the corallite.

To add evidence to stomach analyses and field observations on the role of chaetodontids in subsisting, in part, on living coral, several fish, *C. auriga* and *C. citrinellus*, were placed in aquaria along with living coral heads of *Acropora* sp. The fish quickly nosed down to the surface of the corallum, examined it very carefully, and then neatly nibbled off the polyps. On *Acropora* the terminal polyps on the branches were consumed first, and in a few days a great many of the polyps had been nipped off, leaving white patches on the corallum.

It was also observed that the tubular snouts of these fish were thrust into crevices and interstices in the coral possibly to secure polychaetes or small crustaceans secluded there.

Suyehiro (1942) was rather perplexed about the food and feeding habits of *Chaetodon modestus* from Japan, and concluded that the usual food was hermit crabs and algae. No coral is available to this species, so feeding habits comparable to the Marshallese specimens would not be expected, but the omnivorous nature of *C. modestus* certainly agrees in general with our findings.

Family Acanthuridae

Species: *Acanthurus mata* (surgeon fish, tang)
Number examined: Eniwetok, 1 specimen
Sex: Undeveloped
Standard length: 390 mm
Digestive tract: Mouth small, teeth immovable, close-set, compressed, denticulate; stomach a heavy-walled gizzard; intestine thin-walled, long, coiled

This specimen had taken the following food: Algae—bitten and scraped filamentous algae from a sandy bottom, admixed with a great amount of sand and associated organisms; Foraminifera—several foraminiferans taken were probably picked up along with the sand grains while scraping algae; Gastropoda—minute gastropods, probably also taken incidental to feeding on algae growing on the sand; Detritus. This surgeon fish was commonly seen on the lagoon reef at Eniwetok in 8-10 ft of water over sandy bottoms adjacent to coral mounds. It takes immediate refuge under the coral when approached closely by a swimmer. Its feeding position is head down on compacted sandy bottoms covered with fine, filamentous algae. In the process of scraping off the algae it takes inadvertently numerous minute animals among the benthos. *A. mata* is strictly a grazing herbivore on algal-covered, sandy bottoms.

Species: *Acanthurus xanthopterus* (surgeon fish, tang)
Number examined: Eniwetok, 4 specimens: 2 empty
Sex: Male and female
Standard length: 310-470 mm
Digestive tract: Similar to *A. mata*

The two specimens containing food in their stomachs had the followings items: Algae—short, bitten off filaments with much sand; Coelenterata—Hydroid hydrocaulus; wood splinters. This species is uncommon in the Marshall Islands, but a few were observed at Eniwetok hovering over compacted sandy bottoms on the lagoon reef at depths of 4-50 ft. Its habits are very similar to *A. mata*, feeding frequently in the same area in the same manner.

Species: *Acanthurus gahhm* (surgeon fish, tang)
Number examined: Arno, 1; Eniwetok, 8 specimens
Sex: Males and females
Standard length: 170-215 mm
Digestive tract: Similar to *A. mata*

Food item	*Percentage of fish containing the item*
Algae	
Short, bitten off algal bases with much fine sand	100
Foraminifera	
Calcarina sp., probably taken incidentally to algal browsing on sand	11
Detritus, probably taken incidentally to algal browsing on sand	11

This species is abundant on all reefs with comparatively quiet water 4-40 ft deep. Large schools frequently browse over sandy bottoms, feeding on the fine, short algae growing on the compacted sand. Randall (1956) noted it to behave similarly in the Gilbert Islands.

Species: *Acanthurus olivaceus* (surgeon fish, tang)
Number examined: Arno, 7; Bikini, 1 specimen
Sex: Males and females
Standard length: 57-181 mm
Digestive tract: Similar to *A. mata*

Food item	*Percentage of fish containing the item*
Algae	
Fronds bitten off, with calcareous powder	100
Algal scrapings, with calcareous powder	100
Coralline algae	25
Gastropoda	
Crushed small gastropods	12
Foraminifera	
Calcarina sp.	12

This species is common on the lagoon reefs and leeward ocean reefs in 8-25 ft of water where it swims about coral heads and coral rubble adjacent to compacted, sandy bottoms. Similar habits for this species in the Gilbert Islands were noted by Randall (1956).

During foraging periods this species may feed on the short algal cover on compacted sandy bottoms by swimming head down, or it may scrape algae from coral rubble or the dead bases of coral heads. The gastropods and foraminiferans in the stomach probably are taken inadvertently.

Species: *Acanthurus triostegus triostegus* (convict tang, manini)
Number examined: Arno, 17; Bikini, 1 specimen
Sex: Males and females
Standard length: 42-136 mm
Digestive tract: Similar to *A. mata* except that there is no gizzard, but rather a thick-walled pyloric portion of the stomach.

Food item	*Percentage of fish containing the item*
Algae	
Filaments bitten off, no sand or calcareous dust	100
Scraped filaments, with calcareous dust	5
Foraminifera	
Calcarina sp.	11
Coelenterata	
Scraped coral polyps and skeletal particles	5
Crustacea	
Copepods	5

An ubiquitous, exceedingly abundant surgeon fish on all reefs; sometimes occurring in schools of several hundred busily foraging on the algae of the reef surface. The convict tang is predominantly a browser on algal filaments growing on the reef rock or on bases of dead coral. It apparently grazes only incidentally. The animal constituents of the food probably are inadvertently taken, as this species is strictly herbivorous. Doty & Morrison (1954) report that this species characteristically fed on non-calcareous algae covering dead coral heads (*Pocillopora* sp.) with a brown coating on the reefs of Raroia Atoll, Tuamotus.

The vast numbers of this species on coral reefs provide dynamic evidence of the greater efficiency in energetics for building protoplasm at the lower trophic levels of the food chain.

Species: *Acanthurus achilles* (achilles tang)
Number examined: Bikini, 1; Eniwetok, 2 specimens
Sex: Males and females
Standard length: 130-175 mm
Digestive tract: Similar to *A. t. triostegus*

All three specimens examined contained scraped filamentous algae which was not cropped closely as very little calcareous powder was present. This species is common at the outer edge of the seaward reefs where the surf is strong, and is particularly common in the surge channels. It apparently bites off algal filaments very close to the rocky base; some even appear to be scraped, but the very little calcareous powder found indicates that it is a browser rather than a grazer.

Species: *Acanthurus aliala* (surgeon fish, tang)
Number examined: Arno, 13 specimens
Sex: Males and females
Standard length: 107-162 mm
Digestive tract: Entire digestive tract thin-walled, long, coiled

All specimens examined had consumed algal fronds and filaments which were bitten off, with no sand or calcareous powder admixed. This species is uncommon and rather restricted ecologically to the outer edge of the seaward reef and to surge channels where wave action is moderate to severe. It browses on seaweeds growing in areas of luxuriant coral growth.

Species: *Acanthurus nigroris* (surgeon fish, tang)
Number examined: Arno, 21; Eniwetok, 6 specimens
Sex: Males and females
Standard length: 42-175 mm
Digestive tract: Similar to *A. mata*

Food item	*Percentage of fish containing the item*
Algae	
Fronds and filaments bitten off	96
Algal scrapings, with calcareous powder	11
Algal filaments, admixed with sand grains	3

This small surgeon fish is exceedingly abundant on the lagoon and interisland reefs, as well as in quiet water on the seaward reefs in depths from 2-20 feet. Schultz *et al.* (1953) list this species as *elongatus,* and state that in the northern Marshall Islands it is apparently the most abundant surgeon fish on the reefs; it occurred in almost every type of habitat investigated by them. This species browses on small seaweeds primarily, but does some grazing of short filaments growing both on reef rock and on sandy bottoms. It is more characteristic of coral patches, however, than of reef flats or sandy bottoms.

Species: *Acanthurus guttatus* (surgeon fish, tang)
Number examined: Bikini, 2; Eniwetok, 3 specimens
Sex: Males and females
Standard length: 100-155 mm
Digestive tract: Stomach heavy-walled, not gizzard-like; intestine long, coiled

These specimens contained both fronds and filaments of algae which had been browsed, together with scraped algal filaments admixed with calcareous powder. Consequently, these surgeon fish both browse and graze. Randall (1955) examined several specimens and found them to contain many types of fine algae, *Jania* sp. predominating. The presence of the blue-green alga, *Calothrix,* suggested that they probably crop the algae close to the substrate. The species is abundant on the ocean reef margin, particularly in surge channels, where the current is strong and the water frequently white with bubbles. It frequently ranges up onto the seaward reef flats to forage as the tide rises.

Species: *Acanthurus lineatus* (surgeon fish, tang)
Number examined: Arno, 14 specimens
Sex: Males and females
Standard length: 142-168 mm
Digestive tract: Similar to *A. mata*

These specimens fed predominantly on algal filaments which they browsed, taking little or no calcareous material or sand. The species is, therefore, a browser, with only incidental grazing done. In the Gilbert Islands it was found to subsist mostly on finely divided red algae (Randall 1955). This surgeon fish is rare in the northern Marshall Islands, but locally abundant at Arno Atoll, where it occurred in large schools on the seaward reef flats as the tide arose. Randall (1956) reported it also abundant in the Gilbert Islands. When the seaward reef flats are largely exposed during low tide, schools of this species swim back and forth just beyond the outer reef margin.

Species: *Ctenochaetus striatus* (surgeon fish, tang)
Number examined: Arno, 12; Bikini, 2; Eniwetok, 1 specimen
Sex: Males and females
Standard length: 118-170 mm
Digestive tract: Similar to *A. mata* except for the teeth which are long, slender, moveable and expanded at the tip

Food item	*Percentage of fish containing the item*
Algae	
Algal scrapings, mixed with calcareous powder	80
Algal filaments, mixed with calcareous powder	40
Algal fronds browsed, no sand or calcareous powder	6

This species was common at Arno and at Bikini Atolls, but uncommon at Eniwetok. It occurs on both the lagoon and seaward reefs in shallow water from 6-20 ft deep. It characteristically grazes by scraping dead bases of coral heads and the reef rock, but occasionally forages on the algae growing on the compacted sand adjacent to coral mounds.

Species: *Naso lituratus* (unicorn fish, surgeon fish)
Number examined: Arno, 3; Eniwetok, 6 specimens
Sex: Males and undeveloped
Standard length: 76-390 mm
Digestive tract: Mouth small, teeth bluntly rounded and close-set; stomach thin-walled; intestine long, coiled

Food item	*Percentage of fish containing the item*
Algae	
Fronds and filaments bitten off (mostly *Dictyota* sp.), no sand	67
Fronds and filaments bitten off, admixed with sand	33

This common species of unicorn fish frequents both quiet and turbulent water on the lagoon and seaward reefs 4-30 ft deep. It travels in small schools which browse on the larger seaweeds growing on the rocky substrate, and occasionally on the larger seaweeds growing on compacted sandy bottoms.

Species: *Naso unicornis* (unicorn fish, tang)
Number examined: Arno, 1; Eniwetok, 5 specimens
Sex: Males and females
Standard length: 298-440 mm
Digestive tract: Similar to *N. lituratus*

Food item	*Percentage of fish containing the item*
Algae	
Fronds bitten off, no sand (*Dictyota* sp. and *Padina* sp.)	83
Fronds (*Dictyota* sp.), mixed with calcareous powder	17

This unicorn fish was common in water 3-30 ft in depth on all reefs visited. It usually occurs in small schools which swim about coral heads, especially in the deep, rocky pools on the seaward reefs. This species, like *N. lituratus,* is strictly a browser on the larger seaweeds growing on the rocky flats and coral mounds.

Species: *Zebrasoma veliferum* (surgeon fish, tang)
Number examined: Arno, 1; Eniwetok, 7 specimens
Sex: Males and females
Standard length: 140-260 mm
Digestive tract: Stomach thin-walled, no gizzard; intestine long, coiled

Food item	*Percentage of fish containing the item*
Algae	
Filaments bitten off and scraped, with small amount of calcareous powder	63
Fronds and filaments bitten off, no sand or calcareous powder	37

This species is especially common on the seaward reef in the surf zone, but also occurs on the interisland reefs and the quiet lagoon reefs around living coral patches. It has been observed in water 3-20 ft deep. These fish cruise slowly around coral mounds, now and then nibbling at the algal tufts growing on the bases of coral heads. Frequently, they form large schools and move onto the seaward reef flats as the tide rises. Oftentimes their dorsal fins extend out of water as they crowd each other in their foraging activities in the shallow flats. They are strictly browsers which crop seaweed rather close to its base.

Family Summary

Surgeon fishes, all herbivorous, can be segregated into three feeding types. All species have a long, coiled intestine, and a few species have a heavy-walled, muscular gizzard. The dentition is especially well suited to browsing and grazing algae.

One group, those having a well-developed gizzard (*A. mata, A. olivaceus, A. gahhm,* and *A. xanthopterus*) are habitues of compacted sandy bottoms on which grows a carpet of short algal filaments. Each species characteristically assumes a position with its head downward and caudal fin upward as it grazes the algal mat. Considerable sand is ingested along with the algal filaments, making the gizzard a very effective triturating organ because much of the sand is concentrated there. It is of interest to note that, although apparently distinct species, two of these gizzard-bearing surgeon fish, *A. olivaceus* and *A. gahhm,* have similar color patterns, morphology, and behavior, and the other two species, *A. xanthopterus* and *A. mata,* are also exceeding similar morphologically and behavioristically. Taxonomically *A. olivaceus* and *A. gahhm* have been confused, and *A. xanthopterus* and *A. mata* are rather difficult to distinguish (Randall 1956).

A second group, having no gizzard, but with essentially similar dentition, browses primarily algal fronds and filaments, with some actually grazing the rock surface for fine algal filaments. The latter group nearly always contains a small amount of calcareous powder scraped from the rock surface mixed in with the algae. Among this group, the following species are strictly browsers and rarely, if ever, have any admixed calcareous powder with the algae: *A. t. triostegus, A. achilles, A. aliala, Naso unicornis,* and *Zebrasoma veliferum.* The following species of this group frequently do have calcareous powder admixed with the fine algal filaments, but always have much more browsed algae than that scraped while grazing: *A. lineatus, A. guttatus, A. nigroris,* and *Naso lituratus.*

The third category contains a single species, *Ctenochaetus striatus,* among the acanthurids examined. This species is strictly a grazer on very short and fine algal filaments matted on rocky surfaces. It usually always contains a large proportion of admixed calcareous powder with the algae eaten. The dentition of this species is strikingly different from other genera of surgeon fishes. The teeth which are long, movable, bristle-like, and expanded at the tips, are apparently better adapted for scraping or grazing than for biting or browsing the filaments and fronds.

There is little question that, among the fish fauna on coral reefs in the Marshall Islands, the surgeon fishes are the most important group in converting primary productivity into animal tissue. Their great abundance is ascribable only to the fact that they have more to work with than fish of higher trophic levels in regard to available potential energy, and, whether or not they attain a high percentage of efficiency in the energy transfer, they are able to convert a substantial amount of abundant plant material into fish protoplasm.

Family Scorpaenidae

Species: *Scorpaenodes parvipinnis* (scorpion fish)
Number examined: Bikini, 1 specimen
Sex: Female
Standard length: 60 mm
Digestive tract: Mouth large, teeth minute; stomach thick-walled; intestine medium-long, coiled

The single specimen examined contained an alpheid shrimp in its stomach. These voracious, small carnivores are found in coral mounds almost everywhere on the reefs. They apparently conceal themselves under ledges or in the interstices of coral, lying in wait for small prey to venture close enough to be captured.

Species: *Scorpaenodes* sp. (scorpion fish)
Number examined: Bikini, 2 specimens: 1 empty
Sex: Undeveloped
Standard length: 40-75 mm
Digestive tract: Similar to *S. parvipinnis*

The single specimen containing food in its stomach had eaten several shrimps, the fragments of which remained. The habitat and behavior of this scorpion fish are similar to those described for *S. parvipinnis.*

Species: *Scorpaenopsis gibbosa* (scorpion fish)
Number examined: Arno, 2; Bikini, 1; Eniwetok, 4 specimens: 2 empty
Sex: Males and females
Standard length: 85-150 mm
Digestive tract: Similar to *S. parvipinnis*

Three of the five fish containing food had unidentified fish fragments in their stomachs, another had eaten a small wrasse, and the fifth one had consumed a small parrot fish, *Scarus* sp. This scorpion fish is a sluggish, medium-sized carnivore which lurks beneath coral heads and ledges on both interisland reef shallows and the seaward reef. It lies motionless in wait for small coral fishes and invertebrates to venture closely enough to capture. It is camouflaged as are many other fishes of a sluggish nature, but in addition bears brilliantly colored patches beneath the pectoral fins, suggestive of warning coloration. It reaches a length of about one foot, and has large, pungent dorsal spines which are probably venomous.

Species: *Pterois radiata* (turkey fish, lion fish)
Number examined: Eniwetok, 6 specimens
Sex: Males and females
Standard length: 60-100 mm
Digestive tract: Rather similar to *S. parvipinnis*

Food item	*Percentage of fish containing the item*
Crustacea	
Xanthid crab fragments	50
Stenopus hispidus	16
Alpheid shrimp	16
Shrimp fragments	16

Turkey fish are strikingly-colored, bizarrely-shaped scorpaenids whose sluggish habits and attractive appearance mask one of the most venomous of coral reef fishes in the Marshall Islands. They lurk beneath ledges and in crevices in luxuriant coral beds 3-15 ft deep on all reefs, and are locally very common in some areas. Their extremely poor swimming ability, the result of the highly over-developed impedimenta of the fins, would suggest that the crustaceans taken by them must venture very closely in order that capture can be made. It is not unlikely that the highly colored, greatly elongate and threadlike rays of the fins prove attractive to prey species which are captured when they come close to investigate. The turkey fish seems ''aware'' of its protective ability since it stands its ground when molested.

Species: *Pterois volitans* (turkey fish, lion fish)
Number examined: Eniwetok, 1 specimen
Sex: Undeveloped
Standard length: 230 mm
Digestive tract: Same as *S. parvipinnis*

The single specimen examined had eaten a bandana prawn, *Stenopus hispidus.* The habitat and behavior of this species are essentially similar to those described for *P. radiata.* However, this species is less common, and seems more aggressive or pugnacious than *P. radiata.*

Species: *Synanceja verrucosa* (stonefish)
Number examined: Arno, 2 specimens
Sex: Males
Standard length: 110-176 mm
Digestive tract: Head broad and depressed, mouth superior, cavernous; stomach thick-walled; intestine moderately short

Both specimens examined had consumed fish which were in a late stage of digestion. This species, fortunately uncommon, is found on all reef areas where the water is quiet. It inhabits rocky bottoms where it lies perfectly dormant for long periods of time. It is completely camouflaged because its external morphology, coloring, and shape is stonelike. Stonefish engulf small fish when they venture closely enough by a lightning-fast lunge upward while opening the cavernous mouth to draw them in. The dorsal spines are associated with poison glands and the venom, if not lethal, causes excruciating pain and serious secondary effects.

Family Summary

All scorpion fish, except *Pterois*, have essentially similar habits and feeding methods. In all cases they are sluggish, voracious carnivores, occurring solitarily under ledges or in holes where they await their prey. Except for *Pterois* and *S. gibbosa* they are well camouflaged by color and body sculpture. *S. verrucosa* attains the greatest success in this regard because it habitually lies dormant on rocky bottom and looks exactly like an algal covered rock. *P. radiata* and *P. volitans* appear to be highly colored and morphologically constructed to attract potential prey species. Their venomous spines doubtless serve them well as protection against potential enemies, as their "insolent" behavior suggests.

Family Caracanthidae

Species: *Caracanthus unipinnus*
Specimens examined: Bikini, 1 specimen
Sex: Undeveloped
Standard length: 20 mm
Digestive tract: Mouth moderate in size, teeth minute; stomach large, heavy-walled; intestine short, straight

The specimen examined had eaten an alpheid shrimp. This very small species lives in the interstices of the branches of living coral, particularly *Pocillopora* spp. and *Acropora* spp., on virtually all reefs. It never ventures outside the confines of the coral head where it swims between the branches foraging for other coral-dwelling types. Alpheid shrimps would be particularly common in their diet because they also inhabit the interstices of living corals in great numbers. This caracanthid protects itself from predaceous types by bracing itself between the branches of coral with its exceedingly heavy pectorals.

Family Platycephalidae

Species: *Thysanophrys* sp. (flathead)
Number examined: Bikini, 4; Eniwetok, 8 specimens: 5 empty
Sex: Males and females
Standard length: 82-145 mm
Digestive tract: Head depressed, mouth large, teeth villiform on jaws, canines on palatines, pharyngeal teeth large; stomach thick-walled; intestine moderately short

Food item	*Percentage of fish containing the item*
Crustacea	
Crab fragments	28
Xanthid crab	14
Portunid crab	14
Stenopus hispidus	14
Shrimp fragments	14
Fish	
Unid. fragments	14

This commonly occurring, dorso-ventrally very flattened fish lies on sandy bottoms on all reef areas where it is very well camouflaged. It is a voracious carnivore which lies in wait on exposed, sandy bottoms for small crustaceans and fish to venture closely enough for capture. A rapid lunge with the enormous mouth open is sufficient to capture its comparatively slow-moving prey. In Japan the flathead, *Platycephalus indicus*, feeds exclusively on benthonic fauna including small fish, crabs, polychaetes, and ophiuroids (Suyehiro 1942).

Family Pomacentridae

Species: *Abudefduf sordidus* (damsel fish)
Number examined: Arno, 9; Bikini, 2; Eniwetok, 8 specimens: 1 empty
Sex: Males and females
Standard length: 34-160 mm
Digestive tract: Mouth small, teeth incisiform, uniserial; stomach thick-walled; intestine moderately long, coiled

Food item	*Percentage of fish containing the item*
Algae	
Algal scrapings, with calcareous powder	38
Filaments bitten off, with sand	27
Filaments bitten off, without sand	27
Algal covered pebbles	16
Crustacea	
Crab fragments	16
Shrimp fragments	5
Isopods	5
Amphipods	5
Fish	
Unid. fragments	22
Polychaeta	
Unid. polychaetes	16
Foraminifera	
Calcarina sp.	16
Arachnida	
Mites	5
Coelenterata	
Hydroid fragments	5
Pelecypoda	
Small clam shell fragments	5
Detritus and sand	5

This damsel fish was abundant on all reefs visited, particularly in the shallower portions in depths up to 6 ft. It is especially abundant in large tidepools left by the receding tide on seaward reef flats. The species is gregarious but does not form dense schools.

Its omnivorous habits are obvious from the list of food items consumed, although it is clear that algae form its principal food supply. This damsel fish apparently captures all small benthonic animals encountered while foraging on the algal-covered rocks. It is primarily a grazing species as regards its herbivorous habits. Randall (1955) reports that the one specimen examined in the Gilbert Islands had consumed green algae.

Species: *Abudefduf septemfasciatus* (damsel fish)
Number examined: Bikini, 1 specimen
Sex: Male
Standard length: 135 mm
Digestive tract: Similar to *A. sordidus*

This specimen examined contained the following food items in its stomach: Algae—Fronds bitten off, no calcareous powder; Crustacea—Palaemonid shrimp larva, Copepods; Fish—Unid. fragments.

This solitary damsel fish has habits and occupies a habitat similar to those described for *A. sordidus*. It is likewise omnivorous, although algae formed the bulk of the food in the digestive tract. Two specimens examined by Randall (1955) in the Gilbert Islands had taken only algae, primarily the fine coralline red alga, *Jania* sp.

Species: *Abudefduf leucopomus* (damsel fish)
Number examined: Bikini, 6 specimens
Sex: Males and females
Standard length: 40-55 mm
Digestive tract: Similar to *A. sordidus*

Food item	*Percentage of fish containing the item*
Algae	
Scraped filaments, with much sand and calcareous powder	33
Crustacea	
Copepods, calanoid	33
Mysids	17

Fish	
Unid. fragments	33
Wrasses	17
Gastropoda	
Pteropods	17

This bright yellow damsel fish usually lives solitarily, or in groups of two or three, under rubble on reefs having a rather strong current. It appears to be a true omnivore, taking not only fine algal filaments scraped from the rubble, but also feeding in mid-water on small planktonic crustaceans, pteropods, and smaller fish.

Species: *Abudefduf saxatilis* (sergeant-major)
Number examined: Arno, 1 specimen
Sex: Female
Standard length: 88 mm
Digestive tract: Similar to *A. sordidus*

The single specimen examined contained the following items in its stomach: Algae—Filaments and fronds bitten off, no sand or calcareous powder (intestine nearly filled with algae); Crustacea—Calanoid copepods (numerous), Amphipods (numerous), Isopods (few), Ostracods (few). This species, uncommon in the Marshall Islands, usually occurs solitarily or in small aggregations at the outer edge of the sea reef and in surge channels. It feeds primarily as a browsing herbivore, but the large number of small epiphytic crustaceans leads us to suspect that these are taken more by design than by inadvertence along with the algae.

Species: *Abudefduf dicki* (damsel fish)
Number examined: Arno, 10 specimens: 1 empty
Sex: Males and females
Standard length: 60-72 mm
Digestive tract: Similar to *A. sordidus*

Food item	*Percentage of fish containing the item*
Algae	
Filaments bitten off	55
Filaments scraped off	55
Fish	
Unid. fragments	22
Detritus and sand	22

This solitary damsel fish is found on all reefs with quiet water where it is associated with living corals, particularly the broad, pedestal colonies of *Acropora reticulata* and the staghorn corals representing several species of *Acropora*. It is not at all demersal and swims mostly in mid-water or near the surface. The browsing herbivorous habits of this species predominate, but it is an opportunistic species which will take smaller fish and doubtless swimming invertebrates which venture near it.

Species: *Abudefduf biocellatus* (damsel fish)
Number examined: Arno, 21; Eniwetok, 1 specimen
Sex: Males and females
Standard length: 47-68 mm
Digestive tract: Similar to *A. sordidus*

Food item	*Percentage of fish containing the item*
Algae	
Fronds bitten off, no calcareous powder	33
Filaments scraped off, much calcareous powder	33
Fronds bitten off, admixed with sand	28
Crustacea	
Isopods	9
Cyclopoid copepods	4
Fish	
Unid. fragments	9
Fish eggs	4
Polychaeta	9
Foraminifera	
Calcarina sp.	4

According to some authors (Schultz 1943, Strasburg 1953, Randall 1955) the specimens included under *biocellatus* in this report probably represent a complex of two species, *biocellatus* and *zonatus*. However, it is also possible that *zonatus* may be just a color variant. It is of interest to note that the form considered *biocellatus* abounds in shallow water in depths up to 6 ft on all reefs where rubble is predominant. It prefers hard, conglomerate bottoms, taking refuge under reef rubble when disturbed, and is rarely if ever seen over sandy bottoms. On the other hand, the form referred to as *zonatus* is usually found over sandy bottoms and nowhere else. Because of these different habits Randall (1955) separated the species in his report on fishes of the Gilbert Islands, although he found *biocellatus* only in outer reef areas where coral was abundant. Regardless of the ultimate taxonomic disposition of these species, the food and feeding habits reported here will serve for one or both species. These damsel fish are usually solitary, but sometimes form loose aggregations of two or three individuals. They are primarily herbivores which both browse and graze algae growing on rubble or compacted sand. The cyclopoid copepods, fish fragments, and polychaetes in their diet indicate that they are facultative omnivores as well.

Species: *Abudefduf amabilis* (damsel fish)
Number examined: Arno, 13; Bikini, 5 specimens
Sex: Males and females
Digestive tract: Similar to *A. sordidus*

Food item	*Percentage of fish containing the item*
Algae	
Filaments scraped off, much calcareous powder	38
Fronds bitten off, no sand or calcareous powder	33
Filaments admixed with sand grains	22
Coralline algae	5
Foraminifera	
Calcarina sp.	16
Fish	
Unid. fragments	5
Polychaeta	
Unid. fragments	5

This species occurs in groups of 2-3 individuals primarily on the seaward reef flats in 1-3 ft of water. It is also common on interisland reefs. It prefers areas where the water is in motion, particularly in the area of waves of translation coming across the seaward reef flats on an incoming tide. It will take refuge under pieces of reef rubble. *A. amabilis* may be designated a grazing herbivore primarily on fine algae covering reef rock, although it does browse at times. Like many other damsel fish it is a facultative omnivore.

Species: *Abudefduf glaucus* (damsel fish)
Number examined: Arno, 26; Bikini, 6 specimens
Sex: Males and females
Standard length: 46-75 mm
Digestive tract: Similar to *A. sordidus*

Food item	*Percentage of fish containing the item*
Algae	
Fine filaments, admixed with sand grains	78
Fine filaments, without sand grains	3
Scraped filaments, with calcareous powder	6
Crustacea	
Shrimp fragments	28
Tetralia globerrima	6
Isopods	3
Amphipods	3

Fish	
Unid. fragments	12
Eggs of *Istiblennius* sp.	6
Unid. goby	3
Polychaeta	
Unid. polychaetes	3
Gastropoda	
Cerithium sp.	3
Insect	
Winged ant	3

This common grey or blue damsel fish occurs solitarily or in groups of 2-3 individuals on almost all shallow areas of the reefs where the water is about 3-4 ft deep. It is most prevalent over hard rocky bottoms, and often seeks refuge below large reef rocks. Although it is primarily a grazing herbivore scraping off fine filaments of algae growing on rock surfaces, it very readily becomes a facultative carnivore taking small crustaceans and benthonic forms. The presence of trapezoid crabs and shrimps in about one-half of the specimens examined indicates that they actively seek these forms from the interstices of living heads of branching *Acropora* sp.

Species: *Abudefduf lacrymatus* (damsel fish)
Number examined: Arno, 10; Eniwetok, 4 specimens
Sex: Males and females
Standard length: 39-67 mm
Digestive tract: Similar to *A. sordidus*

Food item	*Percentage of fish containing the item*
Algae	
Fine filaments, with few sand grains	57
Fine filaments, with no sand grains	42
Foraminifera	
Calcarina sp.	14
Unid. species	7
Crustacea	
Copepods	14
Gastropoda	
Crushed small gastropods	7
Fish	
Fish eggs	7

This solitary damsel fish is shy and seen only occasionally despite the fact that it is one of the commonest in shallow reef areas in and around living coral where the water is from 3-12 ft deep. It forages as a browsing herbivore predominantly, with copepods and foraminifera, and possibly even fish eggs and small gastropods, being picked up inadvertently with algae. The crushed gastropods are difficult to explain because the species possesses no dental armature capable of crushing action. Since they are primarily thin-shelled, epiphytic types, it is probable that they were bitten while the fish browsed on the algae.

Species: *Chromis atripectoralis* (coral fish)
Number examined: Eniwetok, 24 specimens: 2 empty
Sex: Males and females
Standard length: 50-68 mm
Digestive tract: Mouth small, teeth with outer row of short canines with two enlarged near symphysis of lower jaw, inner row of teeth villiform; stomach very large, thin-walled; intestine short, straight

Food item	*Percentage of fish containing the item*
Crustacea	
Copepods	85
Shrimp nauplii	61
Small shrimps	33
Mysids	61
Crab zoeae	33
Fish	
Larval fish	4
Polychaeta	
Polychaeta larvae	4
Algae	
Fronds bitten off	4

These brilliant blue coral fish form dense schools about larger branching coral heads, particularly *Pocillopora* sp. and branching *Acropora* sp., in quiet water of the lagoon and leeward ocean reefs. They venture from the coral heads about 3-6 ft, frequently forming a "cloud" of fish about them.

Observations of these schools show the fish to be exceedingly busy capturing small plankters which swarm in the quiet waters of the reefs. The food analysis indicates that copepods, mysids, and shrimp nauplii are most commonly taken, and these can be observed to be the most abundant planktonic food available to them. Although they consume zooplankton, they are not plankton feeders in the sense that they possess structural features which enable them to sieve plankton from the water, but rather represent a carnivorous type which selects particular kinds of plankters which it catches one at a time through visual contact.

Species: *Chromis caeruleus* (coral fish)
Number examined: Arno, 11 specimens: 1 empty
Sex: Males and females
Standard length: 32-49 mm
Digestive tract: Similar to *C. atripectoralis*

Food item	*Percentage of fish containing the item*
Fish	
C. caeruleus eggs	60
Crustacea	
Calanoid copepods	50
Cyclopoid copepods	30
Metanauplii	20
Ostracods	20
Crab zoeae	10
Isopods	10
Sand grains	10

This species, like *C. atripectoralis*, occurs in comparatively large schools in and about interstices of branching corals, particularly *Acropora* sp., in the case of *C. caeruleus*. They are found wherever such corals occur in the quiet waters of the lagoon, interisland, and seaward reefs. Food habits and feeding methods for this species are rather similar to those of *C. atripectoralis*, in that they are a small, mid-water carnivore which feeds primarily on the crustacean elements of the zooplankton in and near the branching corals. It is of interest to note that over one-half of the specimens examined had eaten eggs spawned just previously. All females were gravid and spawning was in full swing. It is not unusual for fish to eat the eggs they have just spawned, and here is a good example of this phenomenon.

Species: *Dascyllus aruanus* (coral fish)
Number examined: Arno, 22 specimens
Sex: Males and females
Standard length: 32-51 mm
Digestive tract: Mouth small, teeth similar to *C. atripectoralis*; stomach thick-walled; intestine medium long, coiled

Food item	*Percentage of fish containing the item*
Crustacea	
Calanoid copepods	72
Copepod metanauplii	36
Cyclopoid copepods	27
Isopods	36
Crab zoeae	22
Shrimp fragments	9
Ostracods	9
Fish	
Fish eggs	45
Unid. fragments	22
Gobies	4
Polychaeta	
Unid. fragments	18
Algae	
Filaments bitten off	59
Filaments scraped, some calcareous powder	4

Frequently large numbers of this species aggregate in branching corals, particularly in *Pocillopora* sp. and *Stylophora* sp. They occur on all reefs where the water is relatively quiet down to a depth of about 15-20 ft. As a swimmer approaches they sink down into the interstices of the coral, remaining there even if the coral head is torn loose and carried ashore. The species is omnivorous, favoring, perhaps, animal food over plant food, but taking a sufficient amount of each to be definitely classed as omnivorous. Its food items are taken both from the mid-water fauna and from the surface of the living coral head and its dead base. The fish eggs taken were spawned in the interstices of the coral, probably by this species itself, although other species place their eggs in such locations.

Species: *Pomacentrus pavo* (damsel fish)
Number examined: Arno, 20 specimens
Sex: Males and females
Standard length: 32-63 mm
Digestive tract: Mouth small, teeth in one series, incisiform; stomach small, heavy-walled; intestine long, coiled

Food item	*Percentage of fish containing the item*
Fish	
Unid. fragments	40
Fish eggs	40
Apogon novemfasciatus	5
Fish scales	5
Crustacea	
Copepods	35
Copepod metanauplii	5
Shrimp fragments	15
Ostracods	10
Isopods	5
Crab zoeae	5
Algae	
Fine filaments, no sand or calcareous powder	10

This more or less solitary pomacentrid is closely associated with living coral mainly in the quiet waters of lagoons at depths of 4-25 ft. Only a few individuals are associated with any one coral head. Although other pomacentrids examined were almost entirely herbivorous, this species is just the reverse and is almost exclusively a carnivore preying upon small fish, crustaceans, and polychaete worms taken either from the mid-water zooplankton or from the interstices of the coral in which it lives. Its rather typical herbivorous-type digestive tract is an enigma.

Species: *Pomacentrus nigricans* (damsel fish)
Number examined: Arno, 19 specimens
Sex: Males and females
Standard length: 52-79 mm
Digestive tract: Similar to *P. pavo*

Food item	*Percentage of fish containing the item*
Algae	
Fine filaments, with sand grains	63
Algal scrapings, with calcareous powder	31
Algal fronds bitten off, no sand or powder	31
Fish	
Unid. fragments	5

P. nigricans is a very abundant species in shallow water around living coral on almost all reefs, where it lives in crevices in the coral. It exhibits very strong territorial tendencies. This species is almost exclusively a grazing herbivore taking fine filaments from the compacted sand surface adjacent to coral patches. The fact that some specimens had fish fragments remaining in the stomach indicates that they can be omnivorous at times.

Species: *Pomacentrus jenkinsi* (damsel fish)
Number examined: Arno, 21 specimens
Sex: Males and females
Standard length: 53-83 mm
Digestive tract: Similar to *P. pavo*

Food item	*Percentage of fish containing the item*
Algae	
Fronds biten off, no sand grains	80
Fine filaments, with sand grains	14
Algal scrapings, with calcareous powder	9
Fish	
Unid. fragments	9
Fish eggs	4

This species is rather uncommon in the northern Marshall Islands, but common at Arno Atoll in the southern Marshalls. It frequents branching corals, either dead or alive, in quiet water of the lagoon and leeward ocean reef shallows to a depth of about 6 ft. It is predominantly a browser on fine algal growth, but grazes at times. It will take animal food as evidenced by its ingestion of both fish eggs and small fish. Its animal food habits are certainly comparatively insignificant.

Species: *Pomacentrus albofasciatus* (damsel fish)
Number examined: Arno, 22 specimens
Sex: Males and females
Standard length: 48-70 mm
Digestive tract: Similar to *P. pavo*

Food item	*Percentage of fish containing the item*
Algae	
Fine filaments, with admixed sand grains	81
Algal scrapings, with calcareous powder	22
Fine filaments, with no sand grains or powder	4
Crustacea	
Shrimp fragments	4
Fish	
Fish eggs	4

This species, common at Arno Atoll, was uncommon in the northern Marshall Islands. It occurs solitarily or in small groups in reef shallows near coral patches where the water is quiet in depths from 3-12 ft. The great quantity of sand admixed with the algae in the digestive tract clearly indicates that this species is a grazer of fine algal filaments on compacted sandy bottoms where it apparently crops very closely, and gets large quantities of sand along with the algae. It also grazes on rocks and dead coral surfaces. Like other pomacentrids it can be a facultative omnivore and takes small crustaceans on occasion.

Species: *Pomacentrus vaiuli* (damsel fish)
Number examined: Arno, 8; Eniwetok, 12 specimens
Sex: Males and females
Standard length: 34-61 mm
Digestive tract: Similar to *P. pavo*

Food item	*Percentage of fish containing the item*
Algae	
Fine filaments, no sand grains	75
Scraped filaments, with calcareous powder	15
Fish	
Unid. fragments	10
Fish eggs	10
Crustacea	
Copepods	10
Amphipods	5
Polychaeta	5

This solitary species lives in crevices and is abundant about living coral patches in water 4-15 ft deep on all reefs. Although it is primarily a browsing herbivore, it frequently behaves omnivorously, and takes small fish and invertebrates occurring in the branching coral heads where it lives.

Family Summary

The pomacentrids are ubiquitous, usually brilliantly colored, coral fishes characteristic of coral reefs in almost every environment found there. Many are solitary, some form small aggregations, while others occur in dense aggregations which have the cohesive and integrated characteristics of highly developed schools. Almost all of them, particularly the aggregating species, are closely associated with, even ecologically bound to, giant heads of branching corals.

The food habits within the family, and even the structural anatomy of the digestive tract, are quite variable, and it is difficult to segregate them into discrete groups of homogeneous habits as regards food and feeding proclivities. They range from almost exclusive herbivores to exclusive carnivores, with most of the species pursuing an omnivorous life to a greater or lesser degree.

Among those species which feed primarily on algae, both by browsing and grazing with approximately equal facility are *A. dicki*, *A. biocellatus*, *A. amabilis*, *A. glaucus*, *A. lacrymatus*, *P. vaiuli*, *P. albofasciatus*, *P. jenkinsi*, and *P. nigricans*. In every case these species consumed some animal types.

One species, *P. pavo*, is almost exclusively carnivorous, taking fish and crustaceans primarily. This is a solitary species which swims about small boulders and coral mounds on the lagoon reef.

Among the omnivores which take animal food both from mid-water and bottom are *A. septemfasciatus*, *A. leucopomus*, *A. saxatilis*, and *A. sordidus*. Of these, *A. sordidus* is the most completely omnivorous species, taking all types of food. It is abundant on the seaward reef flats and in intertidal pools, in aggregations which are not well enough integrated to qualify as schools.

The three species which feed on zooplankton (*C. caeruleus*, *C. atripectoralis*, and *D. aruanus*) are characteristic dwellers in large, branched coral heads. Often as many as 500-1000 fish of *caeruleus* and *atripectoralis* may aggregate in and about one of these giant, ramose heads. When disturbed, they swim down in amongst the branches of the coral, but normally the swarm of fish extends several feet outward from the head. *D. aruanus*, while exhibiting habits similar to *Chromis*, occurs in much smaller aggregations and in smaller ramose heads. The plankters taken by these species are not sieved out of the water by any special device, but rather are captured individually on sight. These plankters form swarms over the reef shallows in quiet water.

The dentition of the feeders on plankton is somewhat different from that of the herbivorous or omnivorous feeders. The teeth of the former types are conical and widely spaced, whereas the teeth of the fish belonging to the other genera, *Abudefduf* and *Pomacentrus*, are villiform or incisiform in bands. The latter are adapted for biting (browsing) or scraping (grazing), just as were the teeth of the herbivorous surgeon fishes.

Family Labridae

Species: *Epibulus insidiator* (wrasse)
Number examined: Bikini, 1; Eniwetok, 1 specimen
Sex: Undeveloped
Standard length: 125-130 mm
Digestive tract: Mouth not produced, but highly protractile, jaws extending backward beneath head; canines at symphyses of jaws; stomach thick-walled; intestine short

Both specimens examined had eaten alpheid shrimps. This species is not common and those taken were from the seaward reef in channels containing living coral. It doubtless occurs elsewhere on the reefs, particularly in coral patches on interisland reefs. This wrasse habitually feeds in ramose corals by extending its exceedingly protractile snout into the interstices to capture small alpheid shrimps and xanthid crabs living there.

Species: *Gomphosus varius* (wrasse)
Number examined: Arno, 3; Bikini, 4; Eniwetok, 14 specimens: 1 empty
Sex: Females
Standard length: 58-120 mm
Digestive tract: Snout produced, tubular; canines at symphyses of jaws; stomach thick-walled; intestine short

Food item	*Percentage of fish containing the item*
Crustacea	
Alpheid shrimps	40
Shrimp fragments	20
Xanthid crab fragments	35
Trapezia sp.	5
Pelecypoda	
Unid. small clam	5
Gastropoda	
Unid. small gastropods	5
Fish	
Unid. fragments	5
Algae	
Fronds, bitten off	5

This species has recently been combined with *G. tricolor*, with the latter referred to synonymy (Strasburg & Hiatt 1957). Although we did not examine the food of the males of this species (formerly designated *G. tricolor*), it may be assumed that the food predilections are the same as for the females examined by us. Randall (1955) examined two males (=*G. tricolor*) in the Gilbert Islands and found them to contain stomatopods and alpheid shrimps, crustaceans characteristic of branching corals.

These wrasses are uncommon but widely distributed about all reefs with living coral in water up to a depth of about 35 ft. They are more common on lagoon reefs, than elsewhere, usually swimming solitarily with characteristic oar-like movements of the pectoral fins. Their long snout is an effective device for probing into interstices of ramose corals where their crustacean prey conceal themselves.

Species: *Pseudocheilinus hexataenia* (wrasse)
Number examined: Arno, 5; Eniwetok, 4 specimens
Sex: Males and females
Standard length: 38-57 mm
Digestive tract: Mouth small, canines on each side of symphyses, upper pair long, curved outward and backward; stomach heavy-walled; intestine medium long

Food item	*Percentage of fish containing the item*
Crustacea	
Shrimp fragments	22
Copepods	44
Ostracods	11
Isopods	11
Foraminifera	
Calcarina sp.	44
Unid. foraminiferans	11

This small wrasse is common in all living coral patches on all reefs in water 3-10 ft deep. It lives solitarily among the branches of ramose corals and feeds primarily on the benthonic fauna living on rubble and sandy bottoms adjacent to coral patches. The specimens examined at Arno contained only the foraminiferan, *Calcarina* sp., and the stomach and gut were crammed full. It was noted then that this species was probably a selective feeder on *Calcarina* sp., but none of these foraminiferans were found in the digestive tracts of specimens examined from Eniwetok. The latter fish had taken only small, benthonic crustaceans. Our data indicate that this species is probably non-selective among the benthonic fauna, but feeds exclusively on certain abundant, easily available forms.

Species: *Labroides dimidiatus* (wrasse)
Number examined: Arno, 1; Eniwetok, 4 specimens
Sex: Females and undeveloped
Standard length: 54-68 mm
Digestive tract: Deep notch at middle of lower lip with fleshy horn extending forward on each side of lower jaw forming lips; pair of large canines at front of each jaw separated by small teeth at symphyses; stomach thin-walled, large; intestine short, nearly straight

Food item	*Percentage of fish containing the item*
Crustacea	
Calagoid copepods	80
Copepods, free-living	40
Mysids	20
Fish	
Fish scales	20

This solitary, agile, strikingly-colored fish is common on all reefs around living coral to depths of about 15 ft. Its peculiar habits which attract the attention of a skin-diver have been noted by several authors. Randall (1955) states, "It often exhibited an unusual mode of swimming by oscillating the posterior part of the body up and down as if to attract attention. It was seen to dance around other fishes in this manner and to pick at their bodies. The fishes receiving such attention often slowed their swimming or came to a stop. It was thought at the time that the *Labroides* were picking off external parasites from these fishes. The gut contents of two specimens from the Gilbert Islands and three from the Marshall Islands consisted of calagoid copepods and a few fish scales. The two remaining Gilbert Islands specimens had eaten tiny isopods along with several fish scales."

Our results fit closely with those obtained by Randall, indicating that the parasitic copepod "picking" from other fish is its predominant mode of feeding, but that it can also take other mid-water plankters. The role of the cleft lower jaw in feeding is not understood. Smith (1953) refers to this species in African waters as one which feeds on minute organisms on rocks, and has been observed to nibble over the mouthparts and gill-covers of large rock-cods.

Species: *Novaculichthys taeniourus* (wrasse)
Number examined: Eniwetok, 1 specimen
Sex: Female
Standard length: 102 mm
Digestive tract: Mouth moderately small, canines at symphyses of both jaws; stomach not well-defined; intestine short, almost straight

The single specimen examined contained on alpheid shrimp in its stomach. This is an uncommon species which occurs solitarily on almost all sandy-bottomed and rubble-strewn reefs at depths of 4-20 ft. It seldom ventures more than a few feet from bottom rubble which serves it as shelter, and is never seen around living coral.

Species: *Stethojulis axillaris* (wrasse)
Number examined: Arno, 17; Eniwetok, 4 specimens
Sex: Males and females
Standard length: 44-75 mm
Digestive tract: Mouth moderately small, no canine teeth, small incisiform teeth in sides of jaws, pharyngeal teeth strong, rounded; stomach not well-defined; intestine rather short

Food item	*Percentage of fish containing the item*
Polychaeta	
Unid. polychaetes	61
Crustacea	
Cyclopoid copepods	38
Calanoid copepods	19
Harpacticoid copepods	9
Copepod metanauplii	14
Cypris larvae	14
Isopods	33
Shrimp fragments	33
Ostracods	19
Xanthid crab fragments	14
Foraminifera	
Calcarina sp.	23
Gastropoda	
Unid. small gastropods	4
Algae	
Fine filaments with sand grains	14
Sand grains	19

This extremely abundant labrid occurs solitarily in shallow water on nearly all reefs. It lives along the bases of coral mounds and patches adjacent to sandy bottoms. It is obviously a non-selective carnivore which forages mostly on the benthonic fauna of sandy areas. It does, however, take some planktonic copepods which it must capture in mid-water.

Species: *Stethojulis* sp. (wrasse)
Number examined: Eniwetok, 6; Arno, 5 specimens
Sex: males and undeveloped
Standard length: 70-95 mm
Digestive tract: Similar to *S. axillaris*

Food item	*Percentage of fish containing the item*
Crustacea	
Isopods	72
Copepods	54
Cypris larvae	9
Ostracods	45
Shrimp fragments	27
Crab zoeae	9
Gastropoda	
Crushed small gastropods	45
Polychaeta	
Unid. polychaetes	18
Foraminifera	
Unid. foraminiferans	18
Pelecypoda	
Crushed small clams	9
Algae	
Filaments scraped, with sand grains	18
Sand grains	81

This species is common on nearly all reefs where it lives, solitarily, around living coral patches adjacent to sandy and rubble-strewn bottoms. It forages for both benthonic and fossorial invertebrates on sandy bottoms, taking primarily crustaceans and polchaetes. The heavy molariform, pharyngeal dentition enables it to crush small hard-bodied species.

Species: *Halichoeres hoeveni* (wrasse)
Number examined: Arno, 1; Eniwetok, 8 specimens
Sex: Female
Standard length: 54-66 mm
Digestive tract: Snout rather pointed, mouth small; symphyses of lower jaw with 1 pair of canines, upper jaw with 2 pairs, pharyngeal teeth molar–like; stomach not well-defined; intestine short

Food item	*Percentage of fish containing the item*
Polychaeta	
Unid. polychaetes	75
Crustacea	
Copepods	50
Isopods	50
Foraminifera	
Calcarina sp.	25
Algae	
Fine filaments of green and coralline algae with much calcareous powder	50

This wrasse is uncommon and is found only in quiet water on the lagoon and leeward ocean reefs at depths of 6-20 ft. It darts about coral heads and usually stays close to the bases of large coral mounds in the lagoon. At Arno Atoll, the single individual examined contained only the foraminiferan, *Calcarina* sp., with which its gut was crammed. However, at Eniwetok different food habits prevailed, with no *Calcarina* taken at all.

Species: *Halichoeres marginatus* (wrasse)
Number examined: Eniwetok, 5 specimens
Sex: Females
Standard length: 48-88 mm
Digestive tract: Similar to *H. hoeveni*

Food item	*Percentage of fish containing the item*
Crustacea	
Isopods	80
Copepods	60
Polychaeta	
Unid. polychaetes	60
Gastropoda	
Crushed gastropods	20
Foraminifera	
Large foraminiferans	20
Algae	
Fine filaments scraped, with sand grains	20

This solitary species is common among luxuriant coral patches in shallow areas on all reefs. It characteristically swims around the top sides of coral heads, only rarely taking refuge when molested. *H. marginatus* may be classed as a benthonic carnivore which usually forages on compacted sandy bottoms, taking mostly small crustaceans and polychaete worms. The algae may have been taken inadvertently during its foraging activities for benthonic fauna in the algal-covered substrate. Its molariform pharyngeals are responsible for crushing the shells of gastropods.

Species: *Halichoeres hortulanus* (wrasse)
Number examined: Arno, 5; Eniwetok, 1 specimen
Sex: Males and females
Standard length: 69-230 mm
Digestive tract: Similar to *H. hoeveni*

Food item	*Percentage of fish containing the item*
Gastropoda	
Crushed gastropods	100
Polychaeta	
Unid. polychaetes	33
Fish	
Unid. fragments	33
Crustacea	
Fragments	17
Hermit crabs, shells crushed	17
Pelecypoda	
Sand-dwelling clams, crushed	17
Algae	
Fine filaments	17

This species is solitary and uncommon, but occurs on all reefs with living coral heads or coral mounds in depths from 3-15 ft. It is a rapid swimmer, seldom taking cover. The food taken indicates that it forages for benthonic and fossorial species, especially hard-bodied forms which it crushes with its heavy pharyngeal teeth. Its primary food consists of small sand-dwelling gastropods, and, in the process of capturing these, it undoubtedly takes many hermit crabs occupying gastropod shells. The shell-crushing habits of this genus are also mentioned by Suyehiro (1942) in his account of *H. poecilopterus* in Japan which bites off barnacles and mussels and then crushes them with its pharyngeal teeth.

Species: *Halichoeres trimaculatus* (wrasse)
Number examined: Arno, 24; Bikini, 6; Eniwetok, 2 specimens
Sex: Males and females
Standard length: 42-120 mm
Digestive tract: Similar to *H. hoeveni*

Food item	*Percentage of fish containing the item*
Crustacea	
Hermit crab fragments, crushed	83
Shrimp fragments	25
Xanthid crab fragments	12
Stomatopod fragments	6
Amphipods	3
Copepods	3
Fish	
Unid. fragments	9
Fish eggs	9
Apogon novemfasciatus	3
Foraminifera	
Calcarina sp.	6
Polychaeta	
Unid. polychaetes	3
Pelecypoda	
Crushed clams	3
Amphineura	
Solenogastrid chiton	3
Algae	
Fine filaments, with sand grains	6

This is the most abundant wrasse on all reefs, particularly favoring sandy bottoms with scattered rubble for cover. It will actually burrow under the sand if molested. Like the other members of this genus, this species is carnivorous on benthonic and fossorial fauna. It has a predilection for hermit crabs which it secures by crushing their shells with the heavy pharyngeal molars. Virtually any prey occurring on sandy bottoms is taken by this fish.

Species: *Halichoeres margaritaceus* (wrasse)
Number examined: Arno, 15 specimens
Sex: Males and females
Standard length: 40-86 mm
Digestive tract: Similar to *H. hoeveni*

Food item	*Percentage of fish containing the item*
Crustacea	
Shrimp fragments	46
Tanaiid isopods	20
Xanthid crab fragments	13
Trapezia sp.	6
Foraminifera	
Calcarina sp.	26
Polychaeta	
Unid. polychaetes	26
Mollusca	
Crushed gastropods	13
Chiton fragments	6
Fish	
Unid. fragments	6
Fish eggs	6

This wrasse is a very abundant, solitary species which occurs in shallow water on all reefs. It is especially abundant at the outer edge of the seaward reefs and in the surge channels. In the lagoon it is found commonly around coral patches 15-20 ft deep. This wrasse feeds less often on sandy bottoms than the other members of the genus examined, and more on and in ramose corals. However, it still is predominantly a feeder on benthonic fauna, but takes no fossorial species as other members of the genus do.

Species: *Macropharyngodon meleagris* (wrasse)
Number examined: Eniwetok, 1 specimen
Sex: Undeveloped
Standard length: 70 mm
Digestive tract: Mouth small, 2 pairs of canines at symphyses of upper and lower jaws, strong canines at corner of upper jaw, pharyngeal teeth molariform; stomach not well-defined; intestine short

The single specimen examined had a crushed rock-dwelling gastropod in its stomach. This small wrasse swims rapidly about coral heads, taking refuge in ramose types in quiet waters of the lagoon and seaward reefs in depths to about 6 feet. It evidently forages on and in coral heads and rocks.

Species: *Macropharyngodon pardalis* (wrasse)
Number examined: Arno, 1; Eniwetok, 3 specimens
Sex: Males and undeveloped
Standard length: 43-57 mm
Digestive tract: Similar to *M. meleagris*

Food item	*Percentage of fish containing the item*
Gastropoda	
Crushed rock-dwelling gastropods	75
Foraminifera	
Calcarina sp.	25
Unid. foraminiferans	25
Sand grains	25

This small, solitary species is very common over living coral on leeward ocean reefs and lagoon reefs in water 3-5 ft deep. It secludes itself in crevices in coral. The Arno specimen had fed exclusively on foraminiferans characteristic of sandy bottoms; whereas, the Eniwetok specimens fed exclusively on rock-dwelling gastropods which were crushed by the heavy pharyngeal teeth. It would appear that this species forages either on sand or rock bottoms, taking hard-bodied species which it can crush.

Species: *Thalassoma umbrostygma* (wrasse)
Number examined: Bikini, 2 specimens
Sex: Male and female
Standard length: 160 mm
Digestive tract: Mouth small, 1 pair canines at symphyses of jaws, pharyngeals molariform; stomach large, thin-walled; intestine short, straight

One of the specimens examined contained an unidentified fish, the other a stomatopod, *Odontodactylus* sp. This solitary wrasse is most common at the seaward reef front and in the back-ridge trough. It also occurs in the interisland reef shallows about living coral. Randall (1955) reported that this species consumed small crabs in the Gilbert Islands.

Species: *Thalassoma quinquevittata* (wrasse)
Number examined: Arno, 20; Eniwetok, 3 specimens
Sex: Males and females
Standard length: 49-184 mm
Digestive tract: Similar to *T. umbrostygma*

Food item	*Percentage of fish containing the item*
Crustacea	
Crab fragments	52
Shrimp fragments	13
Trapezia sp.	4
Fish	
Unid. fragments	21
Apogon novemfasciatus	8
Gastropoda	
Crushed gastropods	4
Echinodermata	
Echinoid fragments	4
Coelenterata	
Tip of *Pocillopora damicornis*, partially digested	4
Algae	
Short clumps	4

This wrasse is very abundant on all reefs around living coral and rocky rubble to depths of about 15 ft. Like other wrasses, it is solitary. Its consumption of crustaceans which live in the interstices of living coral, a coral-dwelling cardinal fish, and the tip of a ramose coral indicates that coral heads and their bases are its primary foraging areas.

Species: *Thalassoma lucasanum marnae* (wrasse)
Number examined: Eniwetok, 2 specimens
Sex: Undeveloped
Standard length: 44-50 mm
Digestive tract: Similar to *T. umbrostygma*

The two specimens examined contained the following food items: Crustacea—Shrimp larvae, Mysids, Crab zoeae, Copepods. This small common species swims rapidly about large lagoon coral heads in quiet water 3-10 ft deep. It feeds mostly on the abundant plankters in the vicinity.

Species: *Thalassoma hardwickei* (wrasse)
Number examined: Arno, 7; Eniwetok, 4 specimens
Sex: Females
Standard length: 35-100 mm
Digestive tract: Similar to *T. umbrostygma*

Food item	*Percentage of fish containing the item*
Crustacea	
Crab fragments	36
Crab zoeae	18
Crab megalopa	9
Shrimp larvae	18
Hippolytid shrimp fragments	9
Copepods	18
Isopods	9
Fish	
Unid. fragments	27
Belonid	9
Foraminifera	
Several species of pelagic foraminiferans	9

This wrasse is common on all quiet reef areas near living coral where it swims solitarily and actively about the tops and sides of the coral heads. The food consumed suggests that it feeds in and about living corals, at times taking small plankters in mid-water. The small belonid fish among the food items indicates that it is a predacious carnivore.

Species: *Thalassoma lutescens* (wrasse)
Number examined: Arno, 1; Eniwetok, 9 specimens
Sex: Females and undeveloped
Standard length: 57-105 mm
Digestive tract: Similar to *T. umbrostygma*

Food item	*Percentage of fish containing the item*
Crustacea	
Xanthid crabs	30
Tetralia globerrima	10
Shrimp fragments	30
Alpheid shrimp fragments	10
Gastropoda	
Unid. crushed gastropods	20
Atys sp., crushed	10
Polychaeta	
Unid. polychaetes	10
Pelecypoda	
Arca sp., crushed	10
Echinodermata	
Ophiuroid fragments	10
Echinoid fragments	10
Algae	
Fine filaments scraped off	30
Fine scrapings, with calcareous powder	10

This bright yellow, solitary wrasse is common on all shallow reefs areas near living coral. It is particularly common in the lagoon around living coral patches where it swims rapidly about the tops and sides of the coral heads. This species exhibits quite heterogeneous carnivorous activities, feeding sometimes in amongst the ramose corals for small coral-dwelling crustaceans, and at other times apparently taking benthonic species from the sandy bottom. The algae contained in the stomach may possibly be the inadvertent result of foraging for benthonic gastropods and polychaetes.

Species: *Cheilinus oxycephalus* (wrasse)
Number examined: Eniwetok, 5 specimens
Sex: Females and undeveloped
Standard length: 65-75 mm
Digestive tract: Mouth small, 1 pair of canines at symphyses of upper and lower jaws, pharyngeal teeth heavy, molariform; stomach virtually absent; intestine short, nearly straight

Food item	*Percentage of fish containing the item*
Crustacea	
Alpheid shrimp fragments	75
Crab fragments	25
Amphipods	25
Gastropoda	
Small gastropods	50

This is an abundant, medium-sized, solitary wrasse which occurs on all reefs with quiet water. It hides under coral or rocks. It is carnivorous, taking crustaceans living in corals and gastropods frequenting corals and coral mounds.

Species: *Cheilinus chlorourus* (wrasse)
Number examined: Arno, 7 specimens: 1 empty
Sex: Males and females
Standard length: 44-98 mm
Digestive tract: Similar to *C. oxycephalus*

Food item	*Percentage of fish containing the item*
Gastropoda	
Whole or crushed gastropods	66
Crustacea	
Shrimp fragments	50
Polychaeta	
Unid. polychaetes	17
Insecta	
Beetles	17

This is a common, solitary wrasse which is found on all reefs about living coral or rubble. It is a slow swimmer compared to many other wrasses in the same habitat. *C. chlorourus* is carnivorous, subsisting primarily on small gastropods taken from coral heads or the rocky bottom nearby. Most specimens had the lower part of the intestine filled with a solid bolus of gastropod shell fragments.

Species: *Cheilinus trilobatus* (wrasse)
Number examined: Arno, 14; Eniwetok, 1 specimen
Sex: Males and females
Standard length: 74-270 mm
Digestive tract: Similar to *C. oxycephalus*

Food item	*Percentage of fish containing the item*
Fish	
Unid. fragments	59
Apogon novemfasciatus	6
Crustacea	
Crab fragments	40
Hermit crabs	6
Shrimp fragments	26
Gastropoda	
Crushed shells, *Cerithium* sp.	18
Pelecypoda	
Crushed clams	6
Algae	
Small fragments of rock containing algal fronds and filaments	6

This solitary wrasse is common on all reef areas around living coral or rubble, under which it lives. It frequently is seen hovering over the sandy bottom near its shelter. This species is carnivorous, taking fish, crustaceans, and gastropods primarily. The single specimen from Eniwetok had fed predominantly on hermit crabs by crushing their shells with the heavy pharyngeal teeth. It apparently forages rather widely, over and in corals and on sandy and rubble bottoms.

Species: *Coris angulata* (wrasse)
Number examined: Eniwetok, 1 specimen
Sex: Undeveloped
Standard length 265 mm
Digestive tract: Mouth small, 1 pair of canines at symphyses of jaws, pharyngeal teeth heavy, molariform; stomach indistinct; intestine rather short

The alimentary tract of the single specimen examined was filled with crushed, sand-dwelling pelecypods and gastropods. This solitary wrasse is common around living coral on all reefs in water 4-20 ft deep. It feeds almost exclusively on sand-dwelling molluscs which it crushes with its heavy pharyngeal teeth.

Species: *Coris gaimardi* (wrasse)
Number examined: Eniwetok, 2 specimens
Sex: Undeveloped
Standard length: 150-250 mm
Digestive tract: Similar to *C. angulata*

Both specimens examined contained shrimps and small crushed clams and gastropods. The following items were found in addition in at least one of the specimens: isopods, foraminiferans, and polychaetes. This wrasse is uncommon in all areas visited, but is found on all types of reefs around coral patches to depths of 20 ft or more. Clams and gastropods form the bulk of its diet. It is a carnivore which forages on open sandy bottoms, although it stays near coral mounds or rock rubble.

Species: *Hemigymnus melapterus* (wrasse)
Number examined: Eniwetok, 3 specimens
Sex: Female and undeveloped
Standard length: 120-220 mm
Digestive tract: Mouth small, 1 pair of canines at symphyses of jaws, pharyngeal teeth heavy, molariform; stomach indistinct; intestine rather short

All of the specimens examined contained small crushed gastropods. The remaining food items found in lesser quantities were: Crustacea—Tanaiid isopods, Shrimp fragments, Amphipods, Crab fragments, Copepods; Foraminifera—*Calcarina* sp., undet. spp.; Algae—small, green filaments and coralline algal filaments bitten and scraped with considerable calcareous powder. This solitary wrasse, common on all reefs in depths from 4-20 ft around coral heads, is comparatively large. Its food includes both inhabitants of living coral heads and the benthonic fauna on sandy bottoms adjacent to luxuriant coral patches. It is quite possible that the algae found in two of the three specimens had been taken inadvertently.

Family Summary

The wrasses are as typical of coral reefs as the corals themselves. While most species are comparatively small, some (*Cheilinus undulatus*) reach gigantic proportions and constitute some of the largest fish ever seen on reefs. They are mostly brilliantly colored in striking contrast to the luxuriant coral patches over and in which many live. Because of their great abundance and widespread distribution on all reef types, they constitute one of the most important groups of fishes in the food complex. Several species are more typical of reef rubble and compacted sandy bottoms than they are of living coral patches.

Most of the species feed on benthonic invertebrates, particularly those on compacted sandy and rubble bottoms. A generic segregation based on food and feeding habits is not feasible. All have well-developed pharyngeal teeth adapted for crushing action. They habitually take hard-bodied species of clams, gastropods, hermit crabs, brachyurous crabs, sea urchins, heart urchins, and brittlestars, all of which are crushed before entering the stomach.

Two species examined habitually probe living ramose coral heads (*Gomphosus varius* and *Epibulus insidiator*) for the small crustaceans and polychaetes secluded in the interstices. Both have structural modifications to facilitate this mode of foraging; *G. varius* has an elongate, tubular snout, and *E. insidiator* has a highly protractile, tubular buccal apparatus. Both species had eaten invertebrates which could only have been removed from the branching corals with some such mechanism.

The availability of particular types of food had a great influence on some species which were not particularly selective in food items consumed. At Arno Atoll *Pseudocheilinus hexataenia* and *Halichoeres hoeveni* had selectively fed on the foraminiferan, *Calcarina* sp., their stomachs and guts being completely crammed with the partly digested protozoans. However, at Eniwetok where *Calcarina* sp. is not nearly so abundant, these species had consumed mostly crustaceans.

Two species examined appear to be rather selective in that they depart from the more usual mode of benthonic foraging among the wrasses and confine their food-getting to mid-water plankters such as mysids, shrimp zoeae, crab zoeae, copepods, etc., so abundant over the reefs in areas of quiet water. These species, *T. hardwickei* and *T. lucasanum marnae*, have no special plankton feeding mechanism, so must capture each plankter individually on sight.

One species, *L. dimidiatus*, has such a unique method of feeding by "tending" other larger fish and removing the parasitic Copepoda that a detailed account of the process was described under the species account. It is the only wrasse with a considerably modified feeding apparatus. Almost all of them conform to the role of small carnivore on invertebrates inhabiting living coral and the sandy bottoms of the reefs.

Family Scaridae

Species: *Cryptotomus spinidens* (parrot fish)
Number examined: Arno, 1 specimen
Sex: Undeveloped
Standard length: 85 mm
Digestive tract: Mouth moderate in size, teeth not fully united to form a smooth beak; no stomach; intestine long, thin-walled

The single specimen examined contained algal filaments which had been grazed along with a large amount of calcareous powder, and coral polyps admixed with coral skeletal fragments. This solitary parrot fish is rather uncommon on the reefs visited, but occurs around coral mounds and coral patches in quiet lagoon waters from 6-8 feet in depth. Its feeding habits are similar to other parrot fishes which scrape reef rock for algae and living coral heads for the polyps. In this particular case much more algae is consumed than are coral polyps, hence the species is designated a grazing herbivore.

Species: *Scarus bicolor* (parrot fish)
Number examined: Eniwetok, 1 specimen
Sex: Female
Standard length: 265 mm
Digestive tract: Similar to *C. spinidens* except that the teeth are fused into a smooth beak.

The single specimen examined contained both coral polyps and algae admixed with great amounts of calcareous powder and coral skeletal fragments. This is a large, solitary parrot fish commonly seen in the surge channels and just off the edge of the ocean reef front in leeward areas of the atolls. Its food seems to consist more of coral polyps than of algae, hence it is here designated as a grazing omnivore.

Species: *Scarus sordidus* (parrot fish)
Number examined: Arno, 16; Eniwetok, 2 specimens
Sex: Females
Standard length: 61-111 mm
Digestive tract: Similar to *S. bicolor*

Food item	*Percentage of fish containing the item*
Coelenterata	
Coral polyps, with much skeletal material admixed	83
Algae	
Fine filaments, admixed with calcareous powder	27

This very common parrot fish forms large schools on all reefs visited in 3-20 ft of water. It is always associated with living coral patches. Scraping living coral heads seems to be its predominant mode of feeding, although it does take some algal material. It is here designated as a grazing omnivore.

Species: Seven unidentified species of *Scarus*
Specimens examined: Arno, 6; Bikini, 2; Eniwetok, 9 specimens
Sex: Males and females
Standard length: 43-325 mm
Digestive tract: Similar to *S. bicolor*

Eleven specimens of this group had consumed coral polyps admixed with a large amount of skeletal particles, and eight specimens contained in addition algal filaments admixed with a great amount of calcareous powder. These parrot fish may therefore be designated as omnivores, with coral polyp scraping practiced somewhat more frequently than rock scraping for algal filaments.

Family Summary

Unfortunately, the taxonomic treatment of the Scaridae of the Marshall Islands, now in process at the U. S. National Museum, has not appeared in print at this writing, and, except for a few easily recognized species, too much confusion in the literature extant prevents us from making unqualified identifications of the seven species lumped in this report. Our treatment of the group should not be construed to mean that all species are similar in habitat, behavior, or influence in the coral reef community.

All parrot fish examined had scraped coral polyps, mostly from the massive, glomerate corals, particularly members of the coral genera *Porites, Astreapora,* and *Montipora.* The beak marks on these heads, and on the rather smooth, algal covered reef rock, are very striking, and their quantity provides a rough measure of the carrying capacity of the particular reef area. Boulenger (1922) stated that parrot fishes fed mostly on vegetable matter, corals, and hard-shelled molluscs, crushing the latter with their unusual dentition. We have not found them taking molluscs in the Marshall Islands. In Japan, where suitable corals are absent, the parrot fish, *Leptoscarus japonicus*, takes only algae (Suyehiro 1942).

Parrot fish are very common inhabitants of all reef areas with living coral. Most species travel in small schools, although a few are solitary, and others are simply gregarious. Particularly common in the back ridge trough of the seaward reef are three large species which form schools of 10 to 50 individuals. These schools are spaced at rather even intervals of a few hundred feet along the seaward reefs. These schooling species are particularly common in surge channels where they go when the water over the seaward reef becomes shallow at ebb tides.

As swimmers approach large parrot fish they usually move off over sandy bottom patches between coral mounds where, at rather frequent intervals, they are observed to void as feces great masses of calcareous powder. There is little doubt that parrot fish contribute substantially to the formation of fine sand by scraping coral and rock surfaces, digesting the algae and coral polyps, and returning the pulverized rock and skeletal material to the bottom as fecal components.

Family Gobiidae

Species: *Gnatholepis anjerensis* (goby)
Number examined: Arno, 5 specimens
Sex: Males and females
Standard length: 32-40 mm
Digestive tract: Mouth small, inferior, villiform teeth on jaws, pharyngeal teeth heavy; stomach indistinct; intestine long, coiled

Food item	*Percentage of fish containing the item*
Crustacea	
Copepods	100
Copepod metanauplii	20
Ostracods	20
Crustacean fragments	20
Detritus, with admixed sand grains	60
Algae	
Fine filaments, admixed with sand grains	40
Gastropoda	
Crushed small gastropods	20

This small goby is ubiquitous on all quiet, compacted sandy bottoms 3-25 ft in depth on lagoon, interisland, and seaward reefs. It is strongly demersal, lives on the sandy bottoms, and retreats into burrows or under rocks when disturbed. This species is omnivorous, taking any food available to it among the benthos. It also makes use of detritus to a certain extent. The rather heavy pharyngeal teeth enable it to crush small, thin-shelled gastropods and crustaceans.

Species: *Gobius ornatus* (goby)
Number examined: Arno, 13 specimens
Sex: Males and females
Standard length: 31-65 mm
Digestive tract: Similar to *G. anjerensis*

Food item	*Percentage of fish containing the item*
Crustacea	
Copepods	84
Copepod metanauplii	7
Isopods	69
Ostracods	53
Amphipods	7
Polychaeta	
Unid. polychaetes	46
Foraminifera	
Several unid. species	23
Gastropoda	
Atys sp.	15
Algae	
Fine filaments, with sand grains	7
Sand grains	61

This species lives in burrows in compacted sand bottoms 3-25 ft deep wherever the water is quiet. It is carnivorous, feeding almost exclusively on small benthonic species which it catches in a rather selective way, favoring crustaceans and polychaete worms.

Species: *Bathygobius fuscus fuscus* (goby)
Number examined: Arno, 14 specimens: 1 empty
Sex: Males and females
Standard length: 32-66 mm
Digestive tract: Mouth terminal, large, teeth villiform, pharyngeal teeth not heavy; stomach large, thick-walled; intestine short, 1 loop

Food item	*Percentage of fish containing the item*
Crustacea	
Crab fragments	30
Shrimp fragments	23
Polychaeta	
Unid. polychaetes	23
Fish	
Unid. fragments	15
Wrasse	7
Goby	7
Insecta	
Ant	15
House fly	7
Algae	
Fine filaments, admixed with sand grains	7

This species is exceedingly abundant, particularly in the intertidal zone on all reefs. It is an ubiquitous inhabitant of the tide pools and shallow depressions. When pursued it leaps from pool to pool, apparently exhibiting a thorough "memory" of its immediate surroundings, since the leaps from pool to pool are accurate and rapid. In addition, it has definite homing tendencies. The fused ventral fins make an effective sucking disc with which it can cling to rock surfaces as the waves surge over it. Its food and feeding characteristics, combined with its digestive morphology, label the species as a carnivore, feeding mostly on the benthonic fauna of tidal flats and the inhabitants of tide pools. Occasionally it will scrape off some algal filaments.

Species: *Gobiodon erythrospilus* (goby)
Number examined: Arno, 5 specimens: 1 empty
Sex: Males and females
Standard length: 28-31 mm
Digestive tract: Mouth terminal, small; teeth villiform with some canines on inner row of lower jaw, 2 pairs rather strong near the symphysis; stomach large, heavy-walled; intestine short

Two of the four specimens examined contained only fish eggs, one of the others contained only isopods, and the fourth had a polychaete worm. This goby lives exclusively in the interstices of living heads of ramose corals (*Pocillopora* sp., *Acropora* sp., *Stylophora* sp.), and thus is found commonly on all quiet reefs where these corals occur in shallow water. Each head seems to have 1-10 individuals within it. They will not leave the coral head, even after it has been taken from the water. The heavy diet of fish eggs resulted from our sampling during the time when several species of coral-inhabiting fish were spawning. Since several of these fish spawn in the interstices of living corals, it is not unusual for the eggs to be eaten by such carnivorous coral-dwelling inhabitants. They also take small crustaceans and polychaetes which inhabit living corals.

Species: *Gobiodon rivulatus* (goby)
Number examined: Arno, 11 specimens: 3 empty
Sex: Males and females
Standard length: 21-33 mm
Digestive tract: Similar to *G. erythrospilus*

Food item	*Percentage of fish containing the item*
Crustacea	
Copepods	50
Copepod metanauplii	25
Isopods	25
Polychaeta	
Unid. polychaetes	25
Detritus and fine sand grains	12

This species occupies the same habitat in the same reef areas as does *G. erythrospilus*. Frequently, a single coral head will contain both species. As a matter of fact, it is entirely possible that what we identified as *G. rivulatus* may be a mixture of two closely-related species, *G. rivulatus* and *G. quinquestrigatus* (Cuvier and Valenciennes). In any event, they appear to have very similar carnivorous food predilections, taking small inhabitants of the coral heads in which they live. The detritus and fine sand found in one specimen examined probably was taken in as the fish was succumbing to rotenone poisoning.

Species: *Paragobiodon echinocephalus* (goby)
Number examined: Arno, 8 specimens: 5 empty
Sex: Females
Standard length: 12-19 mm
Digestive tract: Similar to *G. erythrospilus* except that both jaws have well-developed canines, and gravid females appeared to have no intestine at all, although it may have been collapsed and enclosed by the distended ovaries.

One of the three specimens with food had shrimp fragments, the other two contained isopods. These minute, highly carnivorous ramose coral-dwelling gobies, occur on all reefs with quiet water and luxuriant coral growth, each head containing 1-10 individuals. The habits of this species are essentially similar to *G. erythrospilus.* Here again there is a complex of very similar forms, other species found in identical habitats being *P. kerri* and *P. melanosomus.* Appearance, habitat, and behavior were very similar for all three forms. The gravid females examined contained no food, nor could we locate any digestive tract. It is possible that it could have been overlooked, should it have been entwined among the ovaries.

Family Summary

Usually solitary, sometimes in pairs, at other times in gregarious aggregations, gobies live in ramose corals, as commensals in burrows made by fossorial shrimps or other forms, or on bottoms of tidepools, tidal flats, or shallow lagoon sandy-bottomed areas. For the most part they are carnivorous, but some are actually omnivorous, taking a considerable amount of fine algal filaments and detritus along with small prey species.

From the standpoint of habitats occupied, and to a lesser extent the type of food items consumed, gobies can be segregated into two groups; those which live exclusively in living ramose coral heads, and those living elsewhere.

The most important tidepool and seaward reef flat inhabitant is *B. f. fuscus,* and in burrows on compacted sandy bottoms are found *G. ornatus* and *G. anjerensis.* The food of these species is predominantly small crustaceans and polychaetes, but *G. anjerensis* consumes far more algae and detritus than any of the others and can be designated an omnivore.

In living, ramose corals, particularly in *Pocillopora, Stylophora,* and *Acropora* heads, are the minute carnivorous species *G. rivulatus, G. erythrospilus,* and *P. echinocephalus.* Their food consists of the neighboring small invertebrates occupying the same coral head.

Suyehiro (1942) reporting on the food and feeding habits of several gobies in Japan, also indicated heterogeneous feeding habits for the various species, accompanied by changes in the nature of the digestive tract. He also showed that the food habits of one species, *Chasmichthys gulosus,* changed markedly during growth, from microplankton as juveniles to copepods as they grew slightly larger, and, as adults, to eating each other mostly, but varying the diet with isopods, amphipods, and nereid worms. Other species were zooplankton feeders (*Pterogobius elapoides elapoides*), diatom feeders (*Boleophthalmus pectinirostris*), and scavengers (*Periophthalmus cantonensis*).

Family Eleotridae

Species: *Valenciennea violifera* (sleeper)
Number examined: Arno, 13; Eniwetok, 5 specimens
Sex: Males and females
Standard length: 40-85 mm
Digestive tract: Mouth large, canine teeth strong in front of both upper and lower jaws, pharyngeal teeth weak; stomach indistinct; intestine long, coiled.

Food item	*Percentage of fish containing the item*
Crustacea	
Copepods	100
Cypris larvae	11
Ostracods	88
Isopods	83
Amphipods	16
Shrimp fragments	5
Gastropoda	
Atys sp.	33
Unid. small gastropods	5
Foraminifera, several species	27
Polychaeta	
Unid. polychaetes	16
Pelecypoda	
Small clams	5
Sand grains	72

This sleeper occurs in pairs which live in permanent burrows in compacted sandy bottoms usually beneath a rock. It plugs its burrow with a ball of algae. It is common on all compacted sandy bottoms in depths up to 15 ft on the lagoon, interisland, and seaward reefs where the water is quiet.

The very long intestine suggests that this species ought to subsist to a considerable extent on detritus, but our results indicate that it is, instead, a carnivorous species which subsists on benthonic invertebrates without being particularly selective among them. Crustaceans form the bulk of its diet, but they also comprise the most abundant benthonic group. The fish can be observed to take in a mouthful of the surface material, sift it, and reject the unwanted portion through the gills while swallowing the remainder.

Species: *Valenciennea strigata* (sleeper)
Number examined: Arno, 9; Eniwetok, 11 specimens: 2 empty
Sex: Males and females
Standard length: 44-116 mm
Digestive tract: Similar to *V. violifera*

Food item	*Percentage of fish containing the item*
Crustacea	
Cyclopoid copepods	66
Harpacticoid copepods	11
Calanoid copepods	5
Copepod metanauplii	11
Ostracods	66
Unid. isopods	50
Tanaiid isopods	5
Cypris larvae	33
Shrimps	5
Mollusca	
Small gastropods and veliger larvae	33
Pelecypoda	
Small clams	5
Echinodermata	
Small echinoids	11
Fish	
Unid. fragments	5
Fish eggs	5
Sand grains	50

The habitat and behavior of this common sleeper is essentially the same as that for *V. violifera.* Both species may be found in the same sandy area. Its food habits are exceedingly heterogeneous, and its diet appears to be those items met as the fish scans the benthos and sifts it for food.

Family Summary

Both species of sleepers examined appear to have virtually identical habits and distribution on the sandy-bottom reefs in quiet water. The sandy bottoms occupied are those in which some rocky rubble is present under which they construct their permanent burrows. In so doing they carry out the sand in their mouths and eject it at the entrance to the burrow. They are rather busy fish, and when not sifting the benthos for food, seem to be engaged in lengthening their burrows. When they retreat into the burrow they pull a ball of algal filaments into its opening to plug the hole. This activity was observed many times on the lagoon reef at Arno in water 2-30 ft deep.

They forage by taking in a mouthful of sand and benthos, apparently sift it, then eject the unwanted portion through the gills. They are certainly not selective feeders, but some species taken must be captured on sight, rather than sifted from the benthonic surface layer. The items taken from sifted sand appear in about the same proportion as they occur naturally in the benthos.

Family Microdesmidae

Species: *Paragobioides grandoculis*
Number examined: Eniwetok, 4 specimens: 2 empty
Sex: Females
Standard length: 88-90 mm
Digestive tract: Mouth large, canines well-developed in rows on both jaws; intestine short.

The two specimens examined had taken a small portunid crab and a larval shrimp. This unusual, elongate fish hovers solitarily over the light sand on lagoon reefs at depths of 6-20 ft or more, where it can be detected only by close inspection because of its slenderness and pale coloration. It remains just a few inches above the substrate, rather motionless, but when approached by a swimmer it dives into a borrow. Whether the burrows are self-constructed or are polychaete tubes was not determined. In laboratory aquaria the species readily entered ''burrows'' made from glass tubing. This microdesmid is a carnivore, taking small crustaceans from the benthos. The well-developed canines and large mouth provide it with an efficient mechanism for catching small prey species.

Family Echeneidae

Species: *Echeneis naucrates* (Pilot fish, shark-sucker)
Number examined: Eniwetok, 1 specimen: empty
Sex: Undeveloped
Standard length: 660 mm
Digestive tract: Mouth large, small, sharp teeth on jaws; stomach and intestine a single broad, straight tube.

The specimen examined contained garbage only, and was one of several remoras frequenting the garbage dump at Eniwetok. Several were observed attached by the elliptical sucker on the dorsal side of the head, to sharks (*Ginglymostoma, C. melanopterus* and *C. menisorrah*) and to a large grouper, *Promicrops lanceolatus*. Frequently it has been suggested that these fish feed on fragments of food which the larger, host fishes drop while they themselves are feeding. Both Jordan (1907) and Boulenger (1922) state that these fish are carnivores, and Suyehiro (1942) examined three specimens, all of which were empty. Recently (Maul 1956) various echeneids have been shown to feed upon ectoparasites presumably removed from the skin of their hosts.

Family Parapercidae

Species: *Parapercis cephalopunctatus* (sand perch)
Number examined: Arno, 19; Bikini, 2; Eniwetok, 4 specimens: 1 empty
Sex: Males and females
Standard length: 70-121 mm
Digestive tract: Mouth moderate in size, jaws heavily armed with recurved canines; stomach large; intestine short, straight.

Food item	*Percentage of fish containing the item*
Crustacea	
Xanthid crabs	54
Maiid crabs	8
Portunid crab fragments	8
Shrimp fragments	25
Palaemonid shrimps	8
Stomatopod fragments	8
Galathea sp.	4
Fish	
Unid. fragments	25
Apogon novemfasciatus	4
Fish eggs	4

Parapercids are common on all reefs visited where they live solitarily under coral heads adjacent to sandy bottoms, or lie motionless on the sand which they closely resemble in pattern and color. This species is a voracious, demersal carnivore which lies in wait for its prey, then, when it is sufficiently close, makes a rapid dash of one or two feet along the bottom or into mid-water to make the capture. Both crustaceans and fish are taken as available.

Species: *Parapercis clathrata* (sand perch)
Number examined: Arno, 2 specimens
Sex: Females
Standard length: 122-126 mm
Digestive tract: Similar to *P. cephalopunctatus*

One of the specimens examined contained shrimp fragments; the other had consumed a portunid crab. This species is uncommon on the reefs visited, but it occupies the same habitat and has a behavior pattern similar to that described for *P. cephalopunctatus*.

Family Summary

Sand perch are solitary fish which lie on exposed sandy bottoms, on rocky surfaces, or just beneath coral heads. Their coloration obliterates them effectively as they lie motionless on the sandy substrate. Because of this feature they feed by lying in wait for crustaceans and small fish to come close to them. They seize their prey with a rapid dart of at most 2-3 ft. Their rather large mouths and recurved canines, together with their feeding methods, are much like those of lizard fish (Synodontidae), except that the dentition of sand perch is somewhat less-developed and they are more sluggish.

Family Blenniidae

Species: *Aspidontus taeniatus* (blenny)
Number examined: Arno, 3 specimens
Sex: Males and females
Standard length: 82-92 mm
Digestive tract: Mouth small, minute teeth on both jaws and 1 pair of enormous, recurved fangs on lower jaw; intestine short.

One of the fish examined contained shrimp fragments, another had consumed fish eggs, and the third contained only gurry in its stomach. The color and color pattern of this brilliantly hued blenny are exceedingly like that of the wrasse, *Labroides dimidiatus*, discussed earlier. It is uncommon, but seen occasionally on the seaward and interisland reefs about living coral patches in depths from 3-6 ft and on the lagoon reef around coral mounds down to a depth of about 20 ft. It frequently lives in pipes, tubes, etc., and usually occurs in pairs. It is one of the few fish which will bite severely if handled. This species is carnivorous, taking small crustaceans and fish, usually from living coral heads. Doty & Morrison (1954) apparently mistook this blenny for *L. dimidiatus* in their description of the blenny's behavior as regards its foraging for parasites on the bodies of parrot fish. The almost perfect mimicry, possibly on the part of this blenny (Randall 1955), would make such mistaken identity easily possible.

Species: *Istiblennius coronatus* (blenny)
Number examined: Bikini, 2; Eniwetok, 3 specimens
Sex: Males and females
Standard length: 73-85 mm
Digestive tract: Mouth large, jaws with numerous fine teeth; intestine very long, coiled.

All of the specimens examined had taken large amounts of detritus and fine sand with many algal filaments admixed. Two specimens also contained the foraminiferan, *Calcarina* sp. This blenny is abundant on the seaward reef flats in the intertidal zone. It occurs only on hard bottoms where it lies with just its head protruding from holes and crevices. It is extremely active and alert. During feeding it apparently scoops up the surface sediments on the hard substrate which consist of fine sand, detritus, fine algal filaments and the organic leptopel which covers the substrate in most reef and shore areas (Strasburg Ph.D. thesis).

Species: ***Istiblennius paulus*** (blenny)
Number examined: Arno, 19; Bikini, 3 specimens: 1 empty
Sex: Males and females
Standard length: 51-130 mm
Digestive tract: Similar to *I. coronatus.*

Food item	*Percentage of fish containing the item*
Detritus and fine sand grains	71
Algae	
Fine filaments, with fine sand	61
Scraped filaments, with fine sand	28
Diatoms	38
Foraminifera	
Calcarina sp.	38
Unid. species	33
Crustacea	
Ostracods	28
Copepods	28
Gastropoda	
Unid. minute gastropods	4

This very abundant species occurs on all hard-bottomed reef shallows. It lives on permanently submerged reef flats in depths of 1-2 ft, and not intertidally as does *I. coronatus.* It is an extremely agile and alert species. Like *I. coronatus, paulus* also lies on the bottom with just its head protruding from its hiding place. *I. paulus* is quite omnivorous, taking primarily detritus, leptopel, and benthonic algae and invertebrates by scraping off the thin, sedimentary layer on the reef rock or on compacted sand. It appears to ingest this benthos without exercising much selection between organisms.

Species: ***Exallias brevis*** (blenny)
Number examined: Bikini, 1 specimen
Sex: Female
Standard length: 80 mm
Digestive tract: Similar to *I. coronatus*

The single specimen examined contained fine, filamentous algae and detritus admixed. This uncommon species is found on both the lagoon and seaward reefs in depths from 4-15 ft near living coral. It hides below the living coral heads, the adults being very demersal; however, the young are pelagic. It is predominantly an herbivore scraping the fine algal filaments from the bases of coral heads and coral rock.

Species: ***Cirripectus variolosus*** (blenny)
Number examined: Bikini, 1 specimen
Sex: Female
Standard length: 70 mm
Digestive tract: Similar to *I. coronatus*

The single specimen examined had taken fine algal filaments with detritus admixed, but no sand grains. This common species occurs most abundantly on the seaward reef flat from about the middle to the outer edge, being more abundant in areas containing much living coral. Apparently it prefers regions having considerable water movement. It lives in small holes in the hard substrate, and frequently is seen swimming actively about living coral. Its food consists of fine algae and the precipitated detritus or leptopel which covers rocks in its living area.

Species: ***Cirripectus sebae*** (blenny)
Number examined: Arno, 9 specimens
Sex: Males and females
Standard length: 25-71 mm
Digestive tract: Similar to *I. coronatus*

Food item	*Percentage of fish containing the item*
Detritus	88
Algae	
Fine filaments, with fine sand grains admixed	77
Diatoms	22
Foraminifera	
Calcarina sp.	33
Ostracoda	22
Gastropoda	
Minute gastropods	11

This abundant species prefers regions of considerable water movement and is found most commonly at the outer reef edge and in surge channels on leeward ocean reefs 3-10 ft deep. There it lives in small holes in the substrate, and is often seen flitting about living coral. It has a tendency to move about the reefs rather than to remain secluded in one hole. This species, like *C. variolosus,* subsists on the organic materials on the surface of the hard substrate, particularly on precipitated detritus and fine algal filaments. In the process of scraping off this sediment, it takes minute animal forms (ostracods, foraminiferans) which occur in the benthos.

Family Summary

These active, small fish are found in most habitats on coral reefs, but most of them prefer the seaward reefs, either on the seaward reef flat, or in surge channels and the back ridge trough.

Most species are morphologically adapted to consume a diet heavy in detritus and fine filamentous algae. With this material, gotten by scraping the sediments and organic covering of rocks or hard bottoms, they secure some minute animal species such as foraminiferans, ostracods, copepods, etc., which comprise part of the benthos. There is little question, however, that their diet must be high in leptopel, and experimental holding of several species in captivity has verified this.

Within the family, however, there are some aberrant types which have very different food and foraging habits. One of these examined, *A. taeniatus,* is strictly carnivorous, taking both crustaceans and fish, and not at all morphologically suited to a diet of detritus and algae. Suyehiro (1942) reported on the feeding habits of three genera of blennies, one of which was entirely herbivorous, and two strictly carnivorous. He remarked about the heterogeneity in digestive morphology and food habits and questioned the taxonomic parameters of the family.

Family Brotulidae

Species: ***Dinematichthys iluocoeteoides*** (brotulid)
Number examined: Arno, 12; Bikini, 4 specimens: 4 empty
Sex: Males and females
Standard length: 34-83 mm
Digestive tract: Mouth large, canines in jaws mumerous and well-developed; stomach heavy-walled; intestine short.

Food item	*Percentage of fish containing the item*
Crustacea	
Shrimp fragments	33
Crab fragments	25
Isopods	8
Ostracods	8
Fish	
Unid. fragments	25
Gurry	8

This brotulid is uncommon, but occurs on all reefs visited. It is present at the leeward ocean reef edge and in the surge channels. In the lagoon it lives in coral mounds in about 8-10 ft of water. It has very secretive habits, none ever having been seen alive by us, and apparently secludes itself in holes or crevices in coral. It is a voracious carnivore, taking mostly crustaceans and fish which venture close to its hiding place. From its appearance and seclusiveness we judge it to be very demersal, probably lying in wait for its prey which it dashes out to capture.

Family Balistidae

Species: *Rhinecanthus rectangulus* (trigger fish)
Number examined: Arno, 4; Bikini, 3; Eniwetok, 1 specimen
Sex: Males and females
Standard length: 50-160 mm
Digestive tract: Mouth small, teeth heavy, incisiform, almost fused, pharyngeal teeth not heavy; stomach heavy-walled; intestine long, coiled.

Food item	*Percentage of fish containing the item*
Algae	
Scrapings and filaments, with much calcareous powder	75
Filaments, without sand	12
Crustacea	
Isopods	37
Thalamita sp.	12
Copepods	12
Gonodactylus sp.	12
Polychaeta	
Unid. fragments	12
Foraminifera	
Calcarina sp.	12

This is a very common trigger fish on the seaward reef shallows and on the interisland reefs. It never strays far from its refuge hole or crevice in the hard bottom. It characteristically forages about the shallow reefs away from living coral. The species is omnivorous, taking algae and crustacea primarily. The crustaceans taken are common residents of the sandy and rubble bottoms.

Species: *Rhinecanthus aculeatus* (trigger fish)
Number examined: Arno, 7; Bikini, 1; Eniwetok, 7 specimens
Sex: Males and females
Standard length: 105-181 mm
Digestive tract: Similar to *R. rectangulus*

Food item	*Percentage of fish containing the item*
Algae	
Scrapings, mixed with minute rocky fragments	93
Algal fronds, bitten off	33
Coralline algal fragments	13
Gastropoda	
Atys sp.	40
Small, crushed gastropods	13
Foraminifera	
Calcarina sp.	40
Crustacea	
Isopods	33
Crab fragments	26
Shrimp fragments	20
Amphipods	6
Polychaeta	
Unid. fragments	20
Pelecypoda	
Crushed clams	6
Fish	
Unid. fragments	13
Chromis caeruleus	6
Coelenterata	
Acropora sp., tips broken off	6

This trigger fish is common on the lagoon and interisland reef shallows, and on the seaward reef only in areas of quiet water. It prefers a compacted sandy bottom or one with rubble near coral mounds. Such a heterogeneous feeder can only be omnivorous with no particular predilections noted. It apparently takes anything organic, whether it be soft-or hard-bodied. Those containing *Acropora* tips had consumed great numbers of them, and the intestine was crammed with the sharp skeletal fragments.

Species: *Balistapus undulatus* (trigger fish)
Number examined: Arno, 12; Eniwetok, 8 specimens
Sex: Males and females
Standard length: 115-205 mm
Digestive tract: Similar to *R. rectangulus* except that teeth in front are much heavier and stronger

Food item	*Percentage of fish containing the item*
Coelenterata	
Acropora sp., living tips of branches	65
Scraped polyps, with much skeletal powder	10
Pavona varians, fragments of living corallum	5
Stylaster sanguineus, fragments	5
Fish	
Unid. fragments	55
Abudefduf biocellatus	5
Crustacea	
Crab fragments	45
Xanthid crab fragments	30
Unid. hermit crab	5
Shrimp fragments	20
Gastropoda	
Crushed shells	45
Crushed vermetid tubes	10
Cypraea carneola, crushed	5
Algae	
Fronds, bitten off	45
Fine filaments and scrapings, with much calcareous powder	35
Coralline algal fragments	15
Echinodermata	
Echinometra mathaei, crushed	15
Eucidarid urchin, crushed	10
Spatangid heart urchin, crushed	5
Tunicata	
Unid. fragments	10
Pelecypoda	
Clam fragments	10
Arca sp., crushed	5
Chama sp., crushed	5

This common trigger fish frequents all deep, quiet reefs with considerable living coral, in depths from 4-20 ft. Its omnivorous habits of a completely heterogeneous nature are evident from the table of food items consumed. Although unselective, specimens were encountered frequently which had consumed a meal entirely of one or two items. This was especially true of those that had broken off living tips of ramose corals, and those that had taken tunicates. The strong teeth are used to break off corals, and to crush gastropods, echinoderms, etc. Even coralline algae had been broken off and consumed. Eight specimens examined by Randall (1955) in the Gilbert Islands had similar food habits, even to tunicate fragments, sea urchins, and *Acropora* sp. tips.

Species: *Balistoides viridescens* (trigger fish)
Number examined: Eniwetok, 2 specimens
Sex: Males
Standard length: 490-515 mm
Digestive tract: Similar to *B. undulatus*

One specimen had consumed mostly the living tips of *Pocillopora damicornis*, but also contained crushed shells of cake urchins (*Clypeaster* sp.) and sea urchins (*Eucidaris metularia*), and crushed boring clams, *Lithophaga* sp. The other specimen had eaten solely starfish of an unidentified genus. This solitary species, though uncommon, is large and striking in shape and coloration. It occurs on lagoon reefs around living coral mounds or over sandy bottoms near living coral patches, and on the seaward reef it is found in sheltered areas near coral mounds. *B. viridescens* is strictly a carnivore, subsisting mostly on living coral and echinoderms.

Species: *Pseudobalistes flavimarginatus* (trigger fish)
Number examined: Arno, 1; Eniwetok, 1 specimen
Sex: Female and undeveloped
Standard length: 190-460 mm
Digestive tract: Similar to *B. undulatus*

The food items consumed by the two specimens examined included: Crustacea—*Lydia annulipes*, Isopods; Gastropoda—crushed *Oliva* sp., crushed unid. gastropods; Foraminifera—*Calcarina* sp.; Tunicata—colonial tunicate fragments. This uncommon, solitary trigger fish grows to about 2 ft in length. It was found on the lagoon and interisland reefs where the water was quiet and 10-30 ft deep. It appears to be entirely carnivorous and not particularly selective about its food items. Although these specimens had eaten no coral tips, it is likely that they do take them on occasion.

Species: *Pseudobalistes fuscus* (trigger fish)
Number examined: Arno, 1 specimen
Sex: Not noted
Standard length: 310 mm
Digestive tract: Similar to *B. undulatus*

This specimen contained the following food items: Echinodermata—Heart urchin fragments; Foraminifera—*Calcarina* sp., *Marginopora* sp., unid. foraminiferans; Gastropoda—Vermetid fragments; Pelecypoda—Protoconchs. This large, solitary trigger fish is uncommon, and is found swimming over sandy bottoms in water 10-20 ft in depth. It swims near the bottom, and takes refuge when molested in piles of coralline rubble or under rocks. This species appears to be entirely carnivorous, taking hard-bodied fossorial echinoderms, and breaking off vermetid tubes from their attachment to rocks.

Species: *Melichthys vidua* (trigger fish)
Number examined: Eniwetok, 1 specimen
Sex: Female
Standard length: 140 mm
Digestive tract: Similar to *B. undulatus*

The single specimen of this species contained the following food items: Algae—bitten and scraped filaments and fronds, with many sand grains and much calcareous powder; Crustacea—Xanthid crab fragments, Copepods; Pelecypoda—Small clams; Gastropoda—Small gastropods. This uncommon, solitary species is found on leeward ocean reef shallows with abundant living coral. There it hovers around living coral heads, and hides under the coral when molested. This trigger fish feeds mostly on algae, with the other animal food items being only incidental from a quantitative standpoint. It may be designated as a grazing herbivore and facultative omnivore.

Family Summary

Trigger fish, in general, adhere to a rather heterogeneous and omnivorous diet. Only the genera *Pseudobalistes* and *Balistoides* were found to be completely carnivorous, and this finding may only be the result of too few being examined. Both *P. flavimarginatus* and *P. fuscus* forage mostly on sandy bottoms taking both benthonic and fossorial forms such as echinoderms, foraminiferans, molluscs, and crustaceans which they crush with their exceedingly strong teeth. *B. viridescens* varies this type of diet with meals of the living tips of ramose and cespitose corals such as *Acropora* and *Pocillopora*.

The other trigger fish examined fed on a great variety of items. One species, *B. undulatus*, apparently takes almost anything organic, soft or hard. In all these species algae comprise a prominent part of the diet, and the intestine is very long in compensation. Admixed with the large amounts of grazed algae are fragments of the living tips of branching corals, crustaceans, fish, and molluscs. Almost all of the hard-bodied organisms had been crushed into small pieces, illustrating the versatility of these fish in making a living on a coral reef.

Especially noteworthy is the fact that these trigger fish make good use of the abundant coral and even the echinoderms, the latter a group of ubiquitous organisms avoided by most predaceous animals, and for a time, thought likely to be rather well removed from the more intricate composition of the food web in coral reef communities.

Family Monacanthidae

Species: *Amanses carolae* (file fish)
Number examined: Arno, 2 specimens
Sex: Male and undeveloped
Standard length: 131-151 mm
Digestive tract: Mouth small, teeth long, heavy, incisiform; intestine long, coiled

One of the two specimens examined had the stomach and gut crammed solely with living tips of *Acropora* sp. which were partly digested. The remaining specimen had mostly fragments of a sponge (Calcispongiae), along with algal filaments and fronds bitten off, coralline algal fragments, and scraped coral polyps admixed with much skeletal material. These uncommon file fish occur on quiet, leeward ocean reefs near the outer edge, where they swim slowly about the luxuriant growth of corals and hide under them when molested. This species is omnivorous, but apparently makes a complete meal of a single item if available in sufficient quantity.

Species: *Oxymonacanthus longirostris* (file fish)
Number examined: Eniwetok, 2 specimens
Sex: Male and female
Standard length: 75 mm.
Digestive tract: Snout very long, pointed, mouth terminal, teeth protrude well beyond lips as long cupped incisors; intestine long, coiled.

Both specimens examined contained only coral polyps bitten off, with no skeletal material admixed. This small file fish is common on the lagoon, interisland, and seaward reefs where luxuriant coral growth occurs. It has been observed to have a very close association with living coral, and large numbers of them have been seen head down in living coral heads. Apparently they are engaged in nibbling off the coral polyps, a feeding method for which their dentition is well adapted. This species can be classed as strictly a carnivore.

Species: *Monacanthus* sp. (file fish)
Number examined: Bikini, 1 specimen
Sex: Male
Standard length: 290 mm
Digestive tract: Similar to *A. carolae*, but with incisors even more strongly developed.

This specimen had the entire digestive tract crammed full of the living tips of ramose and cespitose corals (*Acropora, Pocillopora*). Some coralline algal fragments were admixed. The fragments of coral were large, some over 1 inch in length. The intestine, being very thin-walled, protruded outward in all directions as a result of the long coral fragments contained within it. This species is probably exclusively a carnivore, although on occasion some algae may be taken.

Family Summary

All file fish examined fed almost exclusively on coral, although their feeding methods varied considerably. *O. longirostris*, for example, nibbles off the tips of expanded polyps without touching the corallite. On the other hand, the large file fish, *Amanses carolae*, and *Monacanthus* sp., break off the ends of the branches of such ramose and cespitose species as *Acropora*, *Pocillopora*, and *Stylophora*, and fill the entire gut with these large, sharp fragments so that the organic material may be digested. Many fragments an inch or more in length were removed from intestines having a diameter of only half that. *A. carolae* varies its diet by taking sponges and algae in addition to coral. There is little question that file fishes derive the bulk of their nutriment from living corals, and thus are important in helping to bring into circulation within the food web the abundant corals which serve comparatively few predators in relation to the vast bulk of protoplasm they represent.

Family Ostracionidae

Species: *Ostracion cubicus* (trunk fish)
Number examined: Eniwetok, 6 specimens
Sex: Males and females
Standard length: 125-260 mm
Digestive tract: Mouth small, teeth moderate, slightly inclsiform; intestine very long, coiled.

Food item	*Percentage of fish containing the item*
Algae	
Fine algal scrapings, with calcareous powder	50
Filaments, bitten off	16
Polychaeta	
Unid. polychaetes (sand-dwelling)	50
Gastropods	
Atys sp.	33
Pelecypoda	
Crushed clams	16
Fish	
Unid. fragments	16
Crustacea	
Isopods	16
Xanthid crab fragments	16
Sand grains and foraminiferans	67

Trunk fish commonly inhabit all reefs where the water is relatively quiet at depths of 3-20 ft. They are very weak swimmers, cruising slowly around coral heads, hiding in caves, crevices, etc. They are completely omnivorous, taking what food items they can get, mostly from the sandy bottoms around coral mounds. Except for the algae which was probably growing on the coral mound or rocks, all food items are benthonic. The polychaetes taken are exceedingly abundant in the sandy bottoms of the lagoon just below the surface. As would be expected from its structural design and small mouth, trunk fish food getting proclivities are restricted to sedentary or slow-moving invertebrates.

Family Tetraodontidae

Species: *Arothron mappa* (puffer, balloon fish)
Number examined: Arno, 2 specimens
Sex: Male and female
Standard length: 405-540 mm
Digestive tract: Mouth moderately small, teeth 2 large plates in each jaw forming a beak; intestine very long, coiled.

Both specimens examined had the entire digestive tract distended with large fragments of a sponge. In addition a few other food items listed below had been taken: Tunicata fragments; Gastropoda—Crushed shells; Crustacea—Xanthid crab fragments; Algae—Coralline algal fragments, *Halimeda* branches, *Valonia* sp. This large, reticulated puffer is uncommon, occuring in our collections only from the lagoon reef shallows of Arno Atoll. It apparently stays near the lagoon reef edge in 5-10 ft of water. Its noteworthy feeding on sponges is significant in bringing another, little preyed upon organism into the food web.

Species: *Arothron hispidus* (puffer, balloon fish)
Number examined: Arno, 1 specimen
Sex: Male
Standard length: 300 mm
Digestive tract: Similar to *A. mappa*

The single specimen examined contained the following items in its stomach: Pelecypoda—*Pinctada martensi* (crushed), *Codakia punctata* (crushed), *Valsella auriculata* (crushed), *Isognomon costellatum* (crushed); Coelenterata—fine tips of *Pocillopora damicornis;* Porifera fragments; Tunicata fragments; Crustacea—Xanthid crab fragments; Algae—Coralline algal fragments, *Halimeda* fragments. This puffer is uncommon in the Marshall Islands and occurs mostly in the quiet water of the lagoon near living coral at depths of 4-20 ft. It usually secludes itself under a ledge or in a hole in the coral. This species is omnivorous, though primarily a carnivore. The heterogeneity of food habits indicates that it is an opportunist, taking whatever animal food it can get at the time. Its heavy teeth are well adapted for crushing hard-bodied forms and breaking off branches of living coral.

Species: *Arothron meleagris* (puffer, balloon fish)
Number examined: Arno, 3 specimens
Sex: Female
Standard length: 158-176 mm
Digestive tract: Similar to *A. mappa*

In the Marshall Islands this species is almost exclusively a feeder on live coral. All specimens examined contained many living tips of *Acropora* sp., and the following species of corals were taken by at least one of the specimens examined: *Porites lobata* fragments, *Porites superfusa* fragments, *Goniastrea parvistella* fragments, *Pavona varians* fragments, *Montipora* sp. fragments, Alcyonarian tips. The entire gut in all three specimens was choked with the stony fragments of several species of living coral. This puffer is uncommon in the Marshall Islands, and in our collections was taken only at Arno Atoll. There it frequents lagoon reefs wherever luxuriant growths of coral occur. It secludes itself in holes or crevices, or under the living coral heads.

Species: *Arothron nigropunctatus* (puffer, balloon fish)
Number examined: Arno, 1; Eniwetok, 4 specimens
Sex: Females and undeveloped
Standard length: 120-158 mm
Digestive tract: Similar to *A. mappa*

Except for crab fragments in one specimen and unidentified crushed clams in another, these puffers had eaten only living tips of *Acropora* sp. The stomach and intestine of each specimen were completely crammed with the stony branches, those in the stomach just beginning to undergo digestion, while those in the lower intestine were white and cleaned of the fleshy polyps. This puffer is the most common one in the Marshall Islands where it occurs on all reefs having living coral from 2-20 ft deep. Although it is predominantly a carnivore taking living coral as food, it can and does, on occasion, take other organisms such as crustaceans and molluscs. Randall (1955) examined two specimens in the Gilbert Islands and found them both to contain nothing but bite-sized pieces of living coral.

Species: *Arothron* sp. (puffer, balloon fish)
Number examined: Eniwetok, 4 specimens: 3 empty
Sex: Males and females
Standard length: 420-600 mm
Digestive tract: Similar to *A. mappa*, but with more highly developed upper pharyngeal teeth

The single specimen with food contained nothing but ossicles of the recently digested sea star, *Linckia guildingi*. This puffer, taken off the pier at Eniwetok, was not seen elsewhere by us. It is a very large species, attaining a length of over 2 ft.

Family Summary

The puffers, like the trigger fish, have interesting food habits because they incorporate into the food web so many kinds of food organisms which would not otherwise contribute to higher trophic levels because they are usually avoided as food items by other predators. In our experience no two specimens of the same species of puffer had eaten exactly the same food items, or in the same proportionate quantities. They appear to feed predominantly as opportunists, and virtually nothing alive on the reefs is beyond their capacity for utilization.

Perhaps the most consistently taken food item was living tips of ramose and cespitose corals, and even fragments of glomerate and foliaceous types which require considerable strength to break off from the remaining corallum. One specimen had eaten seven different species of corals. However, living tips of the rather delicate *Acropora* sp. heads seem to be preferred. This genus is the most abundant of the corals, and probably the easiest to break off from the main corallum. Various molluscs, particularly pelecypods growing attached to rocks and dead coral bases, are broken away from their attachment and crushed by the heavy dental armature.

Two specimens examined are especially noteworthy for having fed so extensively on unusual items. In one case, the two specimens of *A. mappa* examined from Arno Atoll, the entire gut was greatly distended, literally bloated with large chunks of sponge. Obviously, this was not a case of the chance taking of an unusual food item by them, because the two puffers were caught on different days on different parts of the reef. In another species of puffer from Eniwetok, yet unnamed, the entire gut was choked with small specimens of the ubiquitous sea star of rocky reefs and coral bases, *Linckia guildingi*.

Family Canthigasteridae

Species: *Canthigaster solandri* (sharp-backed puffer)
Number examined: Bikini, 5; Eniwetok, 11 specimens
Sex: Males and females
Standard length: 38-160 mm
Digestive tract: Mouth small, snout somewhat produced, teeth 2 large plates in each jaw forming a powerful beak; intestine long, coiled.

Food item	*Percentage of fish containing the item*
Algae	
Fronds and scraped filaments, with much calcareous powder	81
Crustacea	
Unid. fragments	12
Isopods	6
Tunicata fragments	12
Fish	
Unid. fragments	6
Polychaeta	
Serpulid polychaete	6
Unid. fragments	6
Foraminifera	
Calcarina sp.	6
Coelenterata	
Bitten off and scraped living tips of *Acropora* sp.	6
Bitten off lobes of alcyonarian coral	6

This sharp-backed puffer is very common, and locally abundant, on Marshallese reefs in all areas around living coral. It is common on the seaward reef shallows in all protected areas. The predominant food taken by these specimens was algae, but the animal composition is sufficient to designate the species as an omnivore. The dentition is especially fitted for scraping algal filaments off rocks and dead coral bases.

Family Diodontidae

Species: ***Diodon hystrix*** (spiny puffer)
Number examined: Arno, 1 specimen
Sex: Undeveloped
Standard length: 320 mm
Digestive tract: Mouth small, teeth in each jaw fused into 1 unit forming a powerful beak; intestine medium long.

The single specimen examined contained the following items: Gastropoda—Crushed shells; Crustacea—Xanthid crab fragments; Foraminifera—*Calcarina* sp.; coarse sand grains. The spiny puffer is rather uncommon on all reefs in the Marshall Islands and occurs where the water is relatively quiet in depths of about 8 ft. It feeds primarily on hard-shelled molluscs and crustaceans which it crushes easily with its heavy teeth and strong jaws. It is strictly a carnivore.

ANALYSIS OF FEEDING HABITS BY FORAGING METHODS

ALGAL FEEDERS

Of evolutionary significance is the fact that the herbivorous feeding habit and associated morphological and physiological changes do not appear in the more primitive fishes considered here, but make their entry with the percomorphs in the Family Mugilidae. This is not surprising, of course, because of the rise of modern bony fishes from highly carnivorous predecessors. Although our evolutionary time scales are somewhat unreliable in dating the rise of the several orders of the Osteichthyes, it is certain that these fishes were prevented from direct utilization of the tremendous plant food resources of the sea for a very long time.

The algal feeders can best be segregated into four categories, depending upon the nature of their algal foraging habits. First, there are a few which subsist to a very large extent, at least, on unicellular algal types. The mullets (Mugilidae) and some blennies (Blenniidae) are significant in this regard. Second, there are grazers on algae which crop very closely to the substrate, taking, more often than not, some of the substrate along with the algae. Here, of course, some of the surgeon fishes (Acanthuridae), damsel fishes (Pomacentridae), gobies (Gobiidae), blennies (Blenniidae), and trigger fish (Balistidae), are important. Third there are browsers which have cutting teeth for biting off bits of fronds or filaments above the substrate. In this category are placed some surgeon fishes (Acanthuridae), damsel fishes (Pomacentridae), and trigger fish (Balistidae). The fourth category includes those fishes which take algal food incidental to other food types which predominate in the diet. Some of the more important members of this group are the butterfly fish (Chaetodontidae), wrasses (Labridae), parrot fish (Scaridae), gobies (Gobiidae), and puffers (Tetraodontidae).

In the following lists the more important species in each category of algal feeding type are indicated:

Unicellular Algae

Family Mugilidae (mullet)—*N. chaptali*, *C. crenilabis*; Family Blenniidae—*I. paulus*.

Grazers

Family Leiognathidae (silver perch)—*G. argyreus;* Family Siganidae (rabbit fish)—*S. rostratus;* Family Acanthuridae (surgeon fish)—*C. striatus, A. olivaceus, A. gahhm, A. guttatus, A. nigroris, A. xanthopterus, A. mata, Z. veliferum, N. lituratus;* Family Pomacentridae (damsel fish)— *P. nigricans, P. jenkinsi, P. albofasciatus, A. sordidus, A. glaucus, A. dicki, A. biocellatus, A. amabilis;* Family Labridae (wrasse)—*H. hoeveni;* Family Gobiidae (goby)—*G. anjerensis;* Family Blenniidae (blenny)—*E. brevis, I. coronatus, C. sebae, I. paulus, C. variolosus;* Family Balistidae (trigger fish)—*B. undulatus, R. rectangulus, R. aculeatus, M. vidua;* Family Monacanthidae (file fish)— *A. carolae;* Family Ostracionidae (trunk fish)—*O. cubicus;* Family Canthigasteridae (sharp-backed puffer)— *C. solandri.*

Browsers

Family Siganidae (rabbit fish)—*S. rostratus;* Family Kyphosidae (pilot fish)—*K. cinerascens;* Family Chaetodontidae (butterfly fish)—*C. ephippium, C. auriga, C. reticulatus, C. flavissimus;* Family Acanthuridae (surgeon fish)—*A. t. triostegus, A. achilles, A. guttatus, A. lineatus, A. aliala, A. nigroris, Z. veliferum, N. unicornis, N. lituratus;* Family Pomacentridae (damsel fish)—*D. aruanus, P. vaiuli, P. jenkinsi, A. saxatilis, A. lacrymatus, A. dicki, A. biocellatus, A. amabilis, A. septemfasciatus;* Family Balistidae (trigger fish)— *B. undulatus, R. aculeatus;* Family Tetraodontidae (puffers)—*A. hispidus.*

Incidental

Family Chaetodontidae (butterfly fish)—*C. vagabundus, C. citrinellus;* Family Pomacentridae (damsel fish)—*A. leucopomus;* Family Labridae (wrasse)—*H. melapterus, T. lutescens, H. hortulanus, H. marginatus, Stethojulis* sp., *S. axillaris;* Family Scaridae (parrot fish)—*C. spinidens, S. bicolor, S. sordidus,* Scarids (7 unid. species); Family Gobiidae (goby)—*B. f. fuscus, G. ornatus;* Family Tetraodontidae (puffer)—*A. mappa.*

Detritus Feeders

Comparatively few species among fishes are detritus feeders. It is apparent that on coral reefs benthonic invertebrates are the chief organisms for converting the particulate and colloidal organic material in the benthonic deposits to animal protoplasm. This food source, in turn, reaches the fishes through the multitude of species which prey upon these benthonic and fossorial invertebrate forms. The following fish species depend to a very large extent upon detritus in its several physical forms for their subsistence: Family Mugilidae (mullet)—*N. chaptali, C. crenilabis;* Family Gobiidae (goby)— *G. anjerensis;* Family Blenniidae (blenny)—*E. brevis, I. coronatus, C. sebae, I. paulus, C. variolosus.*

Scavengers

Only one species in our collections seems to fit the category of a natural scavenger, *Ginglymostoma ferrugineum,* the nurse shark.

Plankton Feeders

No fish examined consumed phytoplankton, but several fed upon zooplankton, and of these only a very few have structural adaptations to facilitate sieving the minute plankters out of the water. The manta ray, *M. alfredi,* is perhaps the most highly adapted plankton feeder of the species encountered, but this species is not actually part of the reef fauna, although it does come into the lagoons and even into comparatively shallow water on the reefs. It is believed that the cephalic fins serve to push plankters toward the wide open mouth in which peculiar organs, known as praebranchial appendages, together with the branchial apparatus, serve as straining devices as do gill rakers in other plankton-feeding fishes.

Among the more abundant small plankton feeders on the reefs are the round herring, *S. delicatulus,* the half-beaks, *H. affinis, H. laticeps,* and the silversides, *A. ovalaua* and *P. pinguis.* All of these species possess rather long, fine gill rakers for sieving out small crustacean and other plankters. One species of silversides examined, *S. temmincki,* has gill rakers only of medium length, and this species was found to feed to a great extent on the benthonic fauna rather than on mid-water plankters.

Several species of pomacentrids and two species of labrids were also found to consume plankters, but did not have special filtering devices. Rather, they selected the plankters eaten by visual means.

The following species examined subsist on zooplankton: Family Mobulidae (manta ray)—*M. alfredi;* Family Dussumieridae (round herring)—*S. delicatulus;* Family Hemiramphidae (half-beaks)—*H. affinis, H. laticeps;* Family Atherinidae (silversides)—*A. ovalaua, P. pinguis, S. temmincki;* Family Pomacentridae (damsel fish)—*D. aruanus, C. caeruleus, C. atripectoralis, P. pavo;* Family Labridae (wrasse)—*T. hardwickei, T. lucasanum marnae.*

Carnivores

Coral reefs of the Marshall Islands are replete with carnivores of all sizes, and with a great variety of prey. The carnivores are segregated below into groups which predominantly, or to a great extent at least, seek their prey among the fossorial fauna, benthonic fauna, or mid-water fauna. Lastly the larger, roving carnivores are segregated into those characteristically dwelling on the reefs, and those deep or open water forms which forage over the reefs at regular or irregular intervals. In some cases carnivorous species forage rather widely and are classed in more than one of the groupings listed.

Carnivores on Fossorial Fauna

Family Ophichthidae (snake eels)—*L. semicinctus, B. sauropsis;* Family Moringuidae (whip eels)—*M. macrochir;* Family Holocentridae (squirrel fish)— *M. microphthalmus, H. diadema;* Family Polynemidae (thread fins)—*P. sexfilis;* Family Lutjanidae (snappers) —*L. gibbus, G. griseus;* Family Sparidae (snapper)— *M. grandoculis;* Family Mullidae (goat fish)—*M. samoensis, P. barberinus;* Family Labridae (wrasse)—*C. gaimardi, C. angulata, C. trilobatus, H. trimaculatus, H. hortulanus, H. marginatus, Stethojulis* sp., *S. axillaris;* Family Balistidae (trigger fish)—*B. undulatus, P. fuscus;* Family Ostracionidae (trunk fish)—*O. cubicus.*

Carnivores on Benthonic Fauna

Family Orectolobidae (carpet sharks)—*G. ferrugineum;* Family Clupeidae (sardines)—*H. kunzei;* Family Muraenidae (moray eels)—*E. zebra, E. leucotaenia, E. polyzona, G. pictus, G. petelli, G. javanicus, G. flavimarginatus;* Family Congridae (conger eels)—*C. noordzieki;* Family Synodontidae (lizard fish)—*S. variegatus, S. gracilis;* Family Bothidae (flounders)—*B. mancus;* Family Holocentridae (squirrel fish)—*M.*

berndti, M. microphthalmus, H. sammara, H. lacteoguttatus, H. microstomus, H. laevis, H. diadema, H. spinifer; Family Syngnathidae (pipe fish)—*C. i. waitei, C. f. conspicillatus;* Family Atherinidae (silversides)—*S. temmincki;* Family Polynemidae (thread fins)—*P. sexfilis;* Family Carangidae (jacks)—*T. crumenophthalmus;* Family Apogonidae (cardinal fish)—*P. quinquelineata, C. macrodon;* Family Serranidae (groupers)—*E. merra, E. fuscoguttatus, E. kohleri, E. hexagonatus, E. macrospilos, E. spilotus, V. louti, C. argus, C. urodelus, A. leucogrammicus, P. truncatus;* Family Pseudochromidae—*P. melas, P. nigricans;* Family Leiognathidae (silver perch)—*G. argyreus;* Family Pempheridae (sweepers)—*P. oualensis;* Family Lutjanidae (snappers)—*L. monostigmus, L. bohar, L. vitta, L. vaigiensis, L. gibbus, G. griseus, L. microdon, G. aureolineatus;* Family Sparidae (snappers)—*M. grandoculis;* Family Mullidae (goat fish)—*M. samoensis, P. trifasciatus, P. barberinus, P. cyclostomus, U. arge;* Family Cirrhitidae (hawkfish)—*C. aprinus;* Family Chaetodontidae (butterfly fish)—*C. auriga;* Family Scorpaenidae (scorpion fish)—*S. parvipinnis, S. gibbosa, S. verrucosa;* Family Platycephalidae (flatheads)—*Thysanophrys* sp.; Family Pomacentridae (damsel fishes)—*P. pavo, P. vaiuli, A. sordidus, A. saxatilis, A. lacrymatus, A. glaucus, A. leucopomus;* Family Labridae (wrasses)—*H. melapterus, C. gaimardi, C. trilobatus, C. chlorourus, P. hexataenia, T. lutescens, T. quinquevittata, T. umbrostygma, M. pardalis, M. meleagris, H. margaritaceus, H. trimaculatus, H. hoeveni, H. hortulanus, H. marginatus, Stethojulis* sp., *S. axillaris;* Family Gobiidae (gobies)—*B. f. fuscus, G. ornatus, G. anjerensis;* Family Eleotridae (sleepers)—*V. violifera, V. strigata;* Family Microdesmidae—*P. grandoculis;* Family Parapercidae (sand perch)—*P. cephalopunctatus, P. clathrata;* Family Blenniidae (blennies)—*A. taeniatus, C. sebae, I. paulus;* Family Brotulidae—*D. iluocoeteoides;* Family Balistidae (trigger fish)—*B. viridescens, B. undulatus, P. fuscus, R. rectangulus, R. aculeatus, P. flavimarginatus;* Family Monacanthidae (file fish)—*A. carolae;* Family Ostracionidae (trunk fish)—*O. cubicus;* Family Tetraodontidae (puffers)—*A. hispidus, A. mappa, Arothron* sp.; Family Canthigasteridae (sharp-backed puffer)—*C. solandri;* Family Diodontidae (spiny puffer)—*D. hystrix.*

Carnivores on Mid-water Fauna

Family Carcharhinidae (gray sharks)—*C. melanopterus, C. menisorrah;* Family Triakidae (smooth dogfishes)—*T. obesus;* Family Belonidae (needle fish)—*S. incisa, S. gigantea;* Family Holocentridae (squirrel fish)—*M. berndti, M. microphthalmus;* Family Aulostomidae (trumpet fish)—*A. chinensis;* Family Fistulariidae (cornet fish)—*F. petimba;* Family Atherinidae (silversides)—*S. temmincki;* Family Carangidae (jacks)—*T. bailloni, C. f. jordani, C. melampygus, E. bipinnulatus, S. sanctipetri;* Family Serranidae (groupers)—*V. louti, P. leopardus, P. truncatus;* Family Lutjanidae (snappers)—*Lethrinus miniatus, Lutjanus monostigmus, Lut. bohar, Lut. vitta, A. virescens;* Family Blenniidae (blennies)—*A. taeniatus;* Family Scombridae (tunas)—*G. nuda, K. pelamis, E. a. yaito;* Family Sphyraenidae (barracudas)—*S. qenie.*

Resident Roving Carnivores

Family Carcharhinidae (gray sharks)—*C. melanopterus, C. menisorrah;* Family Triakidae (smooth dogfish)—*T. obesus;* Family Carangidae (jacks)—*C. f. jordani, C. melampygus;* Family Serranidae (groupers)—*P. truncatus, P. leopardus.*

Transient Roving Carnivores

Family Carcharhinidae (gray sharks)—*C. melanopterus, C. menisorrah;* Family Triakidae (smooth dogfish)—*T. obesus;* Family Carangidae (jacks)—*C. melampygus, E. bipinnulatus;* Family Serranidae (groupers)—*P. leopardus;* Family Lutjanidae (snappers)—*L. bohar, A. virescens;* Family Sphyraenidae (barracudas)—*S. qenie;* Family Scombridae (tunas)—*G. nuda, K. pelamis, E. a. yaito.*

CORAL POLYP FEEDERS

Coelenterates, perhaps because of their nematocysts, do not enter into the food web as intermediate forms in most marine communities, and are rarely mentioned as an influential group of organisms in the complex of ecological affairs. However, in tropical coral reefs where luxuriant coral growth not only dominates the scene as regards providing the physical habitat of countless reef species, but also comprises a substantial portion of the total animal protoplasm present (Odum & Odum, 1955), it would be strange indeed if some provision were not made within the many niches to provide for direct utilization of this food resource.

Three distinct evolutionary trends in dentition among a few families of fish have adapted them for accepting a live coral diet. For example, some butterfly fish (Chaetodontidae) and the filefish, *Oxymonacanthus*, have developed pointed, produced snouts with very small terminal mouths containing fine, incisiform, protruding teeth for biting off individual polyps above the level of the corallite. Other butterfly fish crop the polyps so closely that they scrape off the tips of the individual corallites, and parrot fish (Scaridae) have developed a strong, protruding beak of fused teeth with which they heavily scrape glomerate heads of coral, taking not only the polyps but biting deeply into the calcareous corallum as well. Other groups, particularly the trigger fish (Balistidae) and the puffers (Tetraodontidae) have developed very strong, heavy, protruding teeth (trigger fish) or have them fused into a beak as in the puffers with which the ends of ramose and cespitose coral heads (*Acropora, Pocillopora, Stylophora*) are broken off and ingested. The comparatively small amount of animal tissue in relation to the mass of skeletal material requires that such fish keep the gut well crammed with these broken tips nearly all the time.

The most important members characteristic of these three types of coral feeders are listed below:

Browsers on Coral Polyps

Family Chaetodontidae (butterfly fish)—*C. citrinellus, C. auriga, C. lunula, M. strigangulus;* Family Monacanthidae (file fish)—*O. longirostris.*

Grazers on Living Coral Heads

Family Chaetodontidae (butterfly fish)—*C. vagabundus, C. ephippium, C. citrinellus;* Family Scaridae (parrot fish)—*C. spinidens, S. sordidus, S. bicolor;* Unidentified scarids (7); Family Balistidae (trigger fish)—*B. undulatus;* Family Monacanthidae (file fish)—*A. carolae.*

Feeders on Branching Coral Tips

Family Balistidae (trigger fish)—*B. viridescens, B. undulatus, R. aculeatus;* Family Monacanthidae (file fish)—*A. carolae;* Family Tetraodontidae (puffers)—

A. nigropunctatus, A. meleagris, A. hispidus; Family *Canthigasteridae* (sharp-backed puffers)—*C. solandri.*

OMNIVORES

A large number of fish on Marshallese reefs have omnivorous habits, some of which are facultative omnivores and usually contain both plant and animal tissue in their digestive tracts, but do also, on occasion, take full meals of either plants or animals, whichever appears to be the most available. Another group are those fish which are primarily herbivores or primarily carnivores, but which incidentally delve into the opposite food realm, either by inadvertence through their foraging habits, or by design.

Among the facultative group, the damsel fishes (Pomacentridae), gobies (Gobiidae), trigger fish (Balistidae), and the puffers (Tetraodontidae) are the most important. Within the more incidental group the damsel fishes and parrot fishes appear to be the most important.

The lists below indicate the species examined which most clearly fall into the two categories:

Facultative Omnivores

Family Leiognathidae (silver perch)—*G. argyreus;* Family Chaetodontidae (butterfly fish)—*C. ephippium, C. auriga;* Family Pomacentridae (damsel fish)—*D. aruanus, A. sordidus, A. glaucus, A. leucopomus;* Family Labridae (wrasses)—*H. hoeveni;* Family Gobiidae (gobies)—*G. anjerensis;* Family Blenniidae (blennies)—*I. paulus, C. sebae;* Family Balistidae (trigger fish)—*B. undulatus, R. rectangulus, R. aculeatus;* Family Monacanthidae (file fish)—*A. carolae;* Family Ostracionidae (trunk fish)—*O. cubicus;* Family Tetraodontidae (puffers)—*A. hispidus;* Family Canthigasteridae (sharp-backed puffers)—*C. solandri.*

Incidental Omnivores

Family Chaetodontidae (butterfly fishes)—*C. citrinellus;* Family Pomacentridae (damsel fishes)—*P. vaiuli, A. saxatilis, A. lacrymatus, A. dicki, A. biocellatus, A. amabilis;* Family Scaridae (parrot fishes)—*C. spinidens, S. sordidus, S. bicolor,* Unid. *Scarus* sp.; Family Tetraodontidae (puffers)—*A. mappa.*

HABITAT GROUPS ON MARSHALLESE CORAL REEFS

Anyone visiting coral reefs in the Marshall Islands will at once recognize certain characteristic associations of fishes ecologically tied to particular habitats. To analyze these natural associations we have undertaken to depict by descriptions and illustrations their essential physical and biological features.

TIDEPOOL FAUNA

For purposes of describing tidepool life on Marshallese coral reefs we have divided our account into communities living in supratidal pools, above the mean high water mark, and intertidal pools in between the mean high water mark and the mean low water mark. The supratidal pools are only found on the boulder rampart fringing the windward and semi-windward shores where the waves at high tide splash water into pools in the consolidated beach rock. The intertidal pools are found abundantly on the inner half of the seaward reef flat on the windward and semi-windward shores of the atoll.

The physical conditions in both types of tidepools are far more varied than in habitats continually submerged, as tidepools are exposed not only to very high insolation from the tropical sun, but subject also to frequent periods of intense rainfall during low tides when the water in the pools becomes greatly diluted. For example, three small tidepools sufficiently within the intertidal stratum to contain small fish at Arno Atoll were checked for temperature maxima during sunny periods as the tide receded. The uppermost pool examined was awash only during the highest reaches of the incoming tide, the pool examined midway within the intertidal zone was isolated as the tide receded about half way, whereas the lowermost pool examined was awash only during strong surges at extreme low tide. On one afternoon when the air temperature was 87°F, water in the highest pool was 106°F, in the middle pool 105°F, and in the lower pool 99°F. The lower pool had received two or three tidal washes just prior to taking the temperatures. Fish in the two higher pools (*Istiblennius edentulus, Bathygobius f. fuscus*) were still swimming about, but in the lower pool two convict surgeon fishes (*Acanthurus t. triostegus*) and one blenny (*I. edentulus*) had died.

On a second afternoon with an air temperature of 82° F the three pools had water temperatures of 106°F, 103° F, and 106°F. No fish were dead. On a third afternoon when the air temperature was 88°F the three pools had water temperatures of 102°F, 101°F, and 101°F. The considerable variation of water temperatures in relation to air temperatures appears to result directly from the amount of cloud cover in the period just preceding the observations. The fish species inhabiting the supratidal pools are: Family Muraenidae (moray eels)—*G. pictus;* Family Acanthuridae (surgeon fishes)—*A. t. triostegus,* juveniles; Family Pomacentridae (damsel fishes)—*A. sordidus, A. glaucus;* Family Gobiidae (gobies)—*B. f. fuscus;* Family Blenniidae (blennies)—*Istiblennius edentulus, I. lineatus.* These species are shown in characteristic locations and activities in Fig. 2.

Fish species characteristically inhabiting an intertidal pool are: Family Muraenidae (moray eels)—*G. pictus;* Family Pseudochromidae—*P. nigricans;* Family Acanthuridae (surgeon fish)—*A. t. triostegus,* half-grown; Family Pomacentridae (damsel fishes)—*A. sordidus, A. glaucus;* Family Gobiidae (gobies)—*B. f. fuscus;* Family Blenniidae (blennies)—*I. paulus, I. lineatus, I. edentulus, Rhabdoblennius snowi.* Fish species inhabiting intertidal pools are shown in Fig. 2 in characteristic locations and activities.

In all types of tidepools on Marshallese reefs the substrate contains a heavy layer of particulate matter intermixed with short algal filaments and precipitated detritus. Because of the abundance of food of these types, herbivores and detritus feeders predominate. In each instance, however, a few carnivores occur; the tide-flat moray, *G. pictus,* and the voracious pseudochromid, *P. nigricans,* being the most important. Supratidal pools frequently serve as comparatively safe rearing ponds for species such as the convict surgeon fish, *A. t. triostegus.* However, a considerable mortality occurs in this species when water temperatures range over 100°F.

SEAWARD REEF FLAT FAUNA

The outer half of the seaward reef flat slopes just perceptibly downward to the back ridge trough which is a slightly depressed area always covered with water. Immediately seaward of the back ridge trough is the elevated coralline ridge. A vertical section showing the elevations of the seaward reef flat at Arno Atoll in

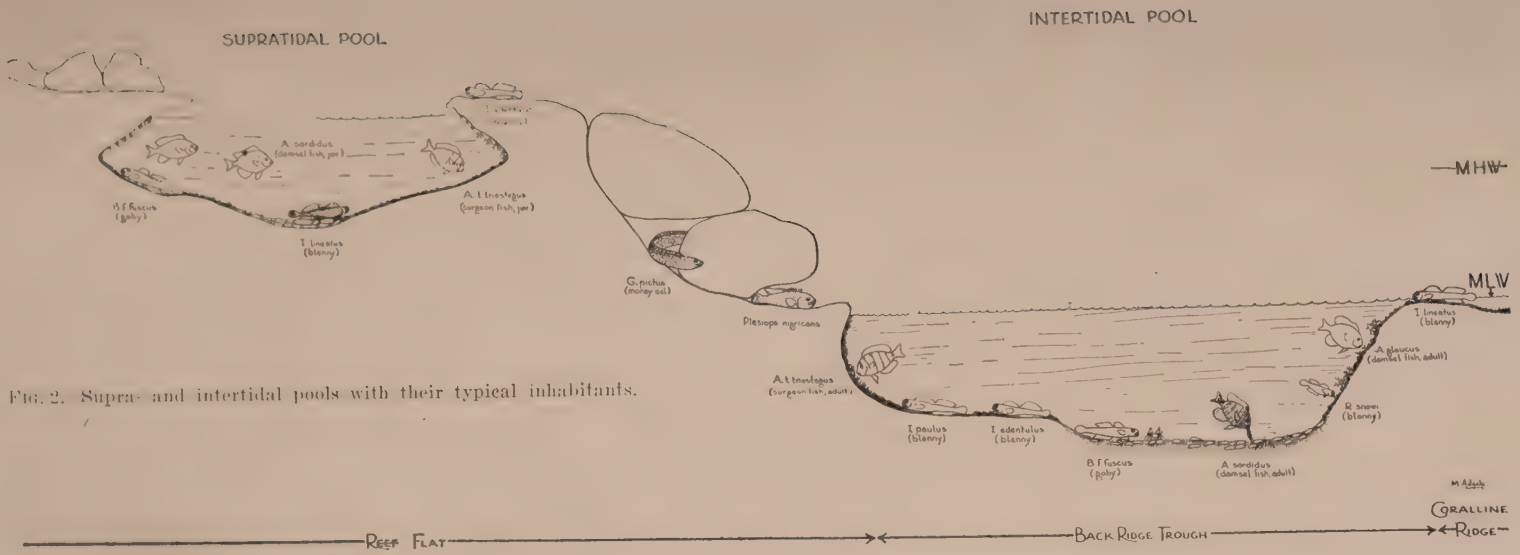
SUPRATIDAL POOL
INTERTIDAL POOL
—MHW—
MLW
A sordidus (damsel fish, juv)
B f fuscus (goby)
T lineatus (blenny)
A. t triostegus (surgeon fish, juv)
G. pictus (moray eel)
Plesiops nigricans
A. t triostegus (surgeon fish, adult)
I paulus (blenny)
I edentulus (blenny)
B f fuscus (goby)
A sordidus (damsel fish, adult)
R snowi (blenny)
A glaucus (damsel fish, adult)
I lineatus (blenny)
M Adachi
REEF FLAT
BACK RIDGE TROUGH
CORALLINE RIDGE

FIG. 2. Supra- and intertidal pools with their typical inhabitants.

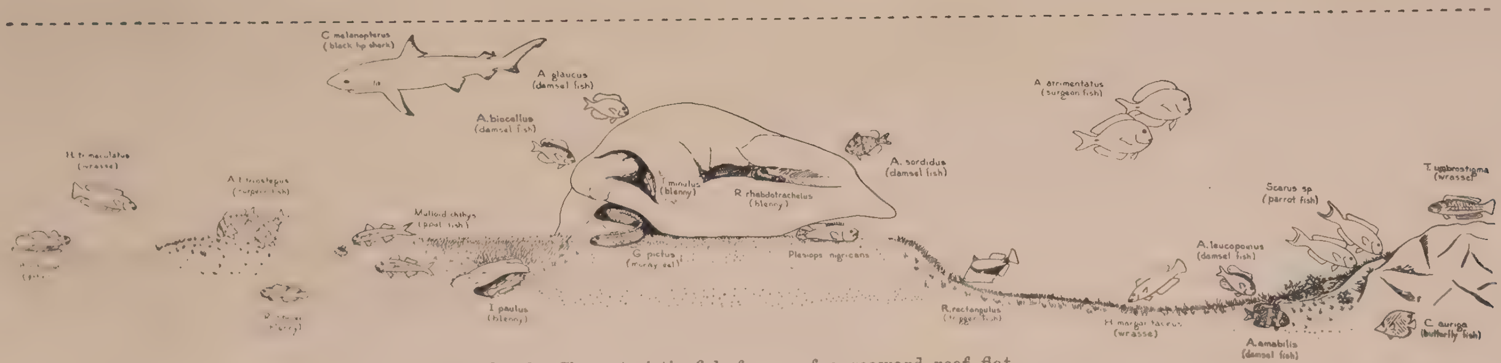
C melanopterus (black tip shark)
A glaucus (damsel fish)
A. biocellus (damsel fish)
H. t. maculatus (wrasse)
A t triostegus (surgeon fish)
Mulloidichthys (goat fish)
I paulus (blenny)
minulus (blenny)
R rhabdotrachelus (blenny)
G pictus (moray eel)
A. sordidus (damsel fish)
Plesiops nigricans
R. rectangulus (trigger fish)
A arimentatus (surgeon fish)
H margaritaceus (wrasse)
A. leucopomus (damsel fish)
A. amabilis (damsel fish)
Scarus sp (parrot fish)
T. umbrostigma (wrasse)
C. auriga (butterfly fish)
M Adachi

FIG. 3. Characteristic fish fauna of a seaward reef flat.

relation to mean sea level has been worked out and submitted for publication (Hiatt, in press).

The outer half of the seaward reef flat is always covered at mean sea level, and is exposed only on certain spring lows, and then only for a few minutes. Ordinarily, the sea swell is adequate to send waves of translation over it even when the tide is exceedingly low. The variations in salinity and temperature are far less than those characteristic for the inshore half of the reef flat.

During low water very little activity, except for the smaller organisms, is evident in this area of the reef. However, as soon as the tide rises sufficiently this region is actually inundated by a horde of larger fish, among them large schools of parrot fish, surgeon fish, goat fish, and small, widely ranging sharks. This intense activity ensues until the water recedes, and these roving types then move out and over the coralline ridge to await along the reef front for the next tidal rise.

The characteristic fishes of this habitat are shown in Fig. 3, and listed below: Family Carcharhinidae (gray sharks)—*C. melanopterus;* Family Muraenidae (moray eels)—*G. pictus;* Family Pseudochromidae—*P. nigricans;* Family Mullidae (goat fishes)—*M. samoensis, U. arge;* Family Chaetodontidae (butterfly fishes)—*C. auriga;* Family Acanthuridae (surgeon fishes)—*A. nigrofuscus, A. t. triostegus;* Family Pomacentridae (damsel fishes)—*A. sordidus, A. glaucus, A. biocellatus, A. amabilis, A. leucopomus;* Family Labridae (wrasses)—*T. umbrostygma, H. margaritaceus, H. trimaculatus;* Family Scaridae (parrot fish)—Several unidentified species of *Scarus;* Family Gobiidae (gobies)—*B. f. fuscus;* Family Blenniidae (blennies)—*I. paulus, Rhabdoblennius rhabdotrachelus;* Family Tripterygiidae—*Tripterygion minutus.*

FAUNA OF THE SURF ZONE AND SURGE CHANNELS

The fish fauna of the outer reef edge and the surge channels, especially on leeward ocean reefs is so varied and complex that it defies adequate description and characterization. A view into one of these surge channels and out over the steep seaward slope is truly one of the most spectacular to be experienced by man. The reef edge and slope are almost solidly covered by over one hundred species of corals of all shapes and hues, and the density and diversity of the fish fauna is exceedingly great. We have made a very feeble attempt at depicting such a scene in Fig. 4.

Because it is manifestly impractical to try to list the fish fauna of this zone, we have selected for presentation only those types most influential in this community. Their characteristic positions and activity are shown in the accompanying figure. Two species are so characteristic of the breaker zone, the sweeper, *Pempheris oualensis,* and the surgeon fish, *Acanthurus guttatus,* that they are here given special notation. *A. guttatus* particularly can be seen in large, fast-swimming schools in the white water of the breaking waves. The sweepers usually occupy positions near the head of shallow channels or just below the white water. The most important species in this habitat are listed below: Family Carcharhinidae (gray sharks)—*C. melanopterus, C. menisorrah;* Family Triakidae (smooth dogfishes)— *T. obesus;* Family Muraenidae (moray eels)—*G. javanicus;* Family Cirrhitidae (hawkfish)—*A. arcatus, P. forsteri;* Family Serranidae (groupers)—*E. merra, P. leopardus, P. truncatus;* Family Pseudochromidae—*P. tapeinosoma;* Family Lutjanidae (snappers)—*L. gibbus;* Family Sparidae (snappers)—*M. grandoculis;* Family Acanthuridae (surgeon fishes)—*A. achilles, A. aliala, A. nigrofuscus, A. lineatus, N. lituratus, N. unicornis, Z. veliferum;* Family Pomacentridae (damsel fishes)—*A. lacrymatus;* Family Labridae (wrasses)—*H. margaritaceus;* Family Scaridae (parrot fishes)—*Scarus* sp. (several); Family Blenniidae (blennies)—*C. sebae, C. variolosus;* Family Balistidae (trigger fish)—*R. rectangulus.*

FISH FAUNA ASSOCIATED WITH ALGAE

Earlier in this report the algal feeders were considered from the standpoint of their actual foraging methods. In this section we shall consider the herbivores as regards their associations with different types of algae growing on both rocky and compacted sandy substrates. The important herbivores in this reef association are shown in their characteristic localities and activities in Fig. 5.

Among the algal feeders are a few which scoop up the surface benthos, sift it to remove the unicellular algae with some admixed detritus for ingestion, and reject the remainder either through the mouth or gill opening. The mullets, *N. chaptali* and *C. crenilabis,* feed entirely in this manner, and can be seen in schools sucking up and sifting the fine benthos on the sandy bottoms.

A rather large group of surgeon fish feeds exclusively on the short filaments of algae growing on the compacted sand. To do this schools of them literally stand on their heads and busily graze on the bottom. Species such as *A. mata, A. xanthopterus, A. gahhm,* and *A. olivaceus* forage in this manner.

Most herbivores browse or graze algae growing on rocky surfaces. Some browse only the larger seaweeds, while many browse and graze the shorter filaments. Among the most important browsers which bite off fronds and filaments from algae growing on rocky surfaces are: rabbit fish (Siganidae), pilot fish (Kyphosidae), butterfly fish (Chaetodontidae), surgeon fish (Acanthuridae), damsel fish (Pomacentridae), and trigger fish (Balistidae). The kinds of algae taken are shown diagrammatically in Fig. 5 and the species are listed in detail under the section on algal feeders considered earlier in this paper.

FISH FAUNA ASSOCIATED WITH LEDGES AND CAVERNS

A swimmer approaching a coral bed is immediately aware of, and greatly impressed by, the large number and variety of fish he sees. However, only a small part of the fish fauna is then in evidence, because most are concealed under rocks or ledges, or are hiding in holes and caverns in the coral itself. It is only after intense searching that some of these species become evident, and only after the area has been poisoned with rotenone that the full impact of the concealed species is felt. No special figure was prepared to show only these species as many of them are visible in our illustrations of other reef situations.

A very large group which remains concealed in coral patches and in rubble is the moray eels. These are primarily ledge and hole dwellers. Another important segment of the fish fauna which inhabits caverns is the squirrel fishes (Holocentridae) which never venture far from their caverns, and usually are seen only in them. They are curious about swimmers, however, and if one watches the opening of a cavern he will see them come up, usually one at a time, take a good look at the swimmer and then disappear again. Also living

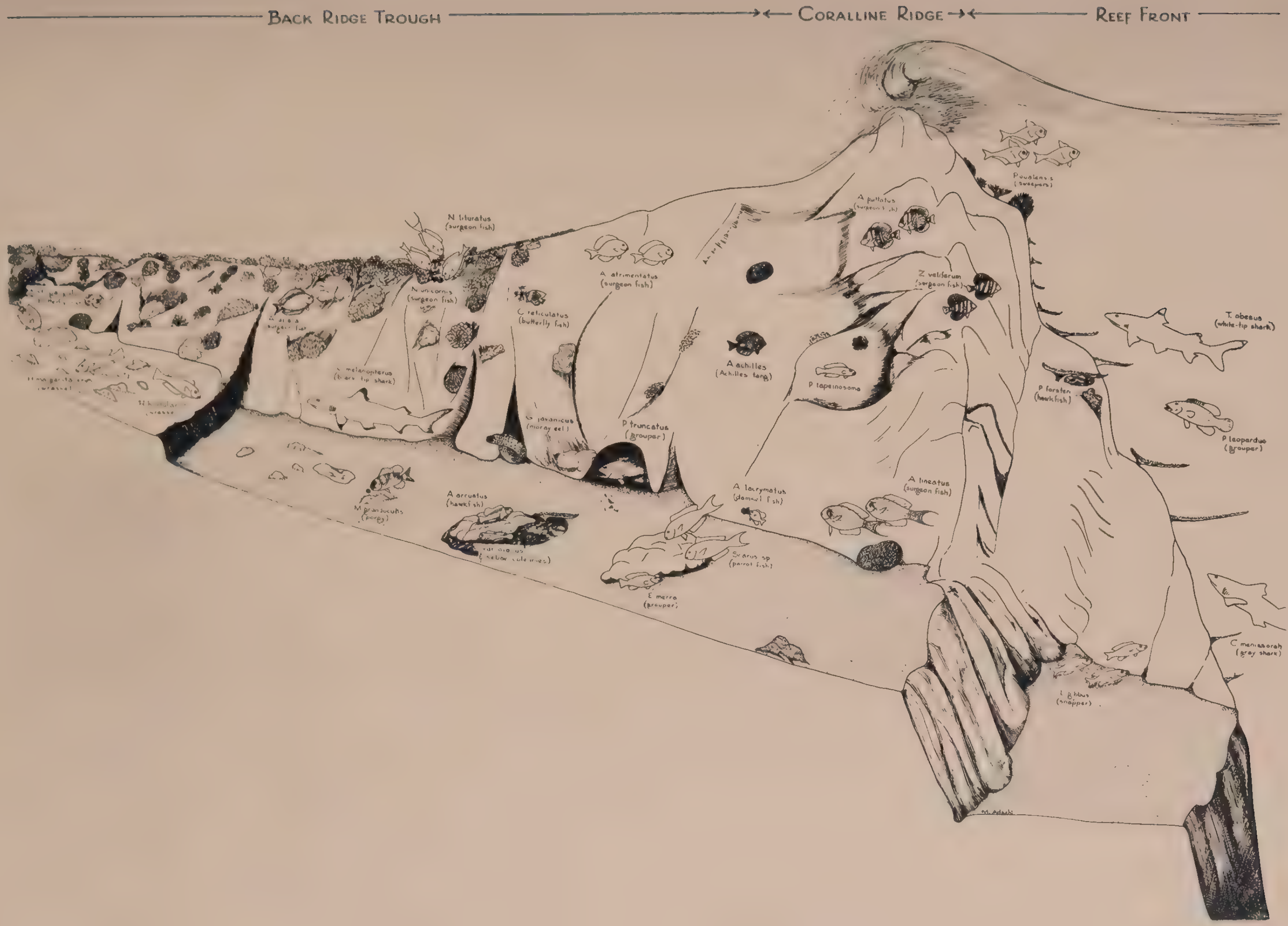
BACK RIDGE TROUGH
CORALLINE RIDGE
REEF FRONT
N. lituratus (surgeon fish)
N. unicornis (surgeon fish)
melanopterus (black tip shark)
C. reticulatus (butterfly fish)
G. javanicus (moray eel)
A. atrimentatus (surgeon fish)
P. truncatus (grouper)
M. grandoculis (porgy)
A. arcuatus (hawkfish)
A. achilles (Achilles tang)
P. tapeinosoma
A. lacrymatus (damsel fish)
Scarus sp. (parrot fish)
E. merra (grouper)
A. guttatus (surgeon fish)
Z. veliferum (surgeon fish)
A. lineatus (surgeon fish)
P. oualensis (sweepers)
T. obesus (white-tip shark)
P. forsteri (hawkfish)
P. leopardus (grouper)
C. menisorrah (gray shark)
L. gibbus (snapper)
M. Adachi

FIG. 4. The fish fauna of a surge channel and the surf zone.

in holes in the coral and in small caverns are many species of cardinal fish (Apogonidae) which frequently hover inside caverns in exceedingly large schools, only venturing out if there is no danger foreseen.

Under ledges and pedestal coral colonies live solitary demersal groupers (Serranidae) of many species, but with similar lying-in-wait foraging techniques, having only the head extended from beneath cover. Although several species of snappers (Lutjanidae) characteristically hide under large coral heads or in ledges, they are not demersal and do not lie in wait for prey. Instead, they forage just a short distance away from their refuge.

A number of the butterfly fishes (Chaetodontidae) also frequent caverns or stay below large coral heads a good deal of the time. Two species holding great attraction for, as well as commanding great respect from, reef biologists are the turkey or lion fish, *Pterois volitans* and *P. radiata.* These venomous species, having greatly elaborated fins and striking coloration, seclude themselves under ledges or corals and have never been seen by us in an exposed situation.

Observations made on the reefs, coupled with a check on the proportion of empty stomachs in fishes caught during the day, indicate that certain of these ledge and cavern dwellers probably have nocturnal foraging proclivities. These species are: Family Muraenidae (moray eels)—*G. pictus, G. flavimarginatus, G. undulatus, G. fimbriatus;* Family Holocentridae (squirrel fishes)—*M. berndti, M. microphthalmus, H. sammara, H. lacteoguttatus, H. microstomus, H. laevis, H. diadema, H. spinifer.*

Ledge and cavern dwellers known to be day foragers are: Family Muraenidae (moray eels)—*E. zebra, E. leucotaenia, E. polyzona, U. xanthopterus, R. marshallensis, G. javanicus, G. buroensis, G. margaritophorus;* Family Congridae (conger eels)—*C. noordzieki;* Family Apogonidae (cardinal fishes)—*A. novemfasciatus, A. snyderi, A. exostigma, A. nigrofasciatus, A. novaeguineae, A. erythrinus, P. quinquelineata;* Family Priacanthidae (big eyes)—*P. cruentatus;* Family Serranidae (groupers)—*E. merra, E. fuscoguttatus, E. kohleri, E. hexagonatus, E. macrospilos, E. spilotus, V. louti, C. argus, C. urodelus, A. leucogrammicus, P. truncatus;* Family Pempheridae (sweepers)—*P. oualensis;* Family Lutjanidae (snappers)—*L. monostigmus, L. vitta, L. vaigiensis, L. gibbus;* Family Chaetodontidae (butterfly fish)—*C. vagabundus, C. ephippium, C. auriga, C. lunula, C. flavissimus, M. strigangulus;* Family Acanthuridae (surgeon fishes)—*C. striatus, A. mata;* Family Scorpaenidae (scorpion fishes)—*P. radiata, P. volitans;* Family Brotulidae—*D. iluocoeteoides.*

Fish Fauna Associated with Mid-water and Surface Communities

Surface and mid-water communities are comparatively distinct, although some larger carnivores range rather widely and enter both areas on occasion. Surface communities are composed primarily of minute zooplankton, larger zooplankton, small plankton-feeding fish, (the round herring, *S. delicatulus,* and silversides, *A. ovalaua* and *P. pinguis*), larger macroplankton feeding fish such as the half-beaks (Hemiramphidae), trumpet fish (Aulostomidae), cornet fish (Fistulariidae), and fish-eating carnivores such as needle fish (Belonidae), tunas (Scombridae), barracuda (Sphyraenidae), and rainbow runner (Carangidae).

In mid-water a number of large, hovering groupers (Serranidae) and snappers (Lutjanidae) occur just above the bottom, and several species of more rapidly swimming roving carnivores such as sharks (Carcharhinidae and Triakidae), jacks (Carangidae), and snappers (Lutjanidae) are usually always present in quiet waters on all reefs. Fig. 6 depicts the important species engaging in their usual activities in the characteristic habitat.

The important species in the surface community are listed below: Family Mobulidae (manta rays)—*M. alfredi;* Family Dussumieridae (round herrings)—*S. delicatulus;* Family Belonidae (needle fishes)—*S. incisa, S. gigantea;* Family Hemiramphidae (half-beaks)—*H. affinis, H. laticeps;* Family Atherinidae (silversides)—*A. ovalaua, P. pinguis;* Family Scombridae (tunas)—*G. nuda, K. pelamis, E. a. yaito;* Family Sphyraenidae (barracuda)—*S. qenie;* Family Carangidae—*S. sanctipetri.*

The important species in the mid-water community are the following: Family Carcharhinidae (gray sharks)—*C. melanopterus, C. menisorrah;* Family Triakidae (smooth dogfishes)—*T. obesus;* Family Holocentridae (squirrel fishes)—*M. berndti, M. microphthalmus;* Family Aulostomidae (trumpet fish)—*A. chinensis;* Family Fistulariidae—*F. petimba;* Family Atherinidae (silversides)—*S. temmincki;* Family Scombridae (tunas)—*G. nuda, K. pelamis, E. a. yaito;* Family Sphyraenidae (barracuda)—*S. qenie;* Family Carangidae (jacks)—*T. bailloni, C. f. jordani, C. melampygus, S. sanctipetri, E. bipinnulatus;* Family Serranidae (groupers)—*V. louti, P. leopardus, P. truncatus;* Family Lutjanidae (snappers)—*L. monostigmus, L. bohar, L. vitta, A. virescens, L. miniatus.*

Fish Fauna Associated with Glomerate Coral Heads

Because glomerate coral heads are generally devoid of interstices in which small organisms can hide, such heads are visited only by fish species intent upon browsing or grazing coral polyps. Most glomerate heads (*Porites, Astreopora, Coscinaraea, Cyphastrea, Goniastrea, Leptastrea, Pavona*) on luxuriant coral reefs are marred by paired tooth scrapings as a result of grazing on them by parrot fishes, trigger fishes, and others. Frequently such tooth marks are exceedingly abundant, indicating that the turnover rate of corals and coral feeding fishes must be running rather close to maximum sustaining capacity.

Fishes which browse the polyps without cropping too closely and getting particles of the calcareous corallite and corallum belong mostly to the family Chaetodontidae (butterfly fish). The most important grazers are the parrot fishes (Scaridae), the trigger fishes (Balistidae), and the puffers (Tetraodontidae).

Fig. 7 depicts the fish activity around a glomerate coral head. The significant species associated with such coral heads, all grazers or browsers except the pipe fish which merely hunt for small crustaceans on the surface of the head, are listed below: Family Syngnathidae (pipe fishes)—*C. i. waitei, C. f. conspicillatus;* Family Chaetodontidae (butterfly fishes)—*C. vagabundus, C. ephippium, C. citrinellus, C. auriga, C. lunula, M. strigangulus;* Family Scaridae—*C. spinidens, S. sordidus, S. bicolor, Scarus* sp. (7 unid. species); Family Balistidae (trigger fish)—*B. undulatus;* Family Tetraodontidae (puffers)—*A. meleagris.*

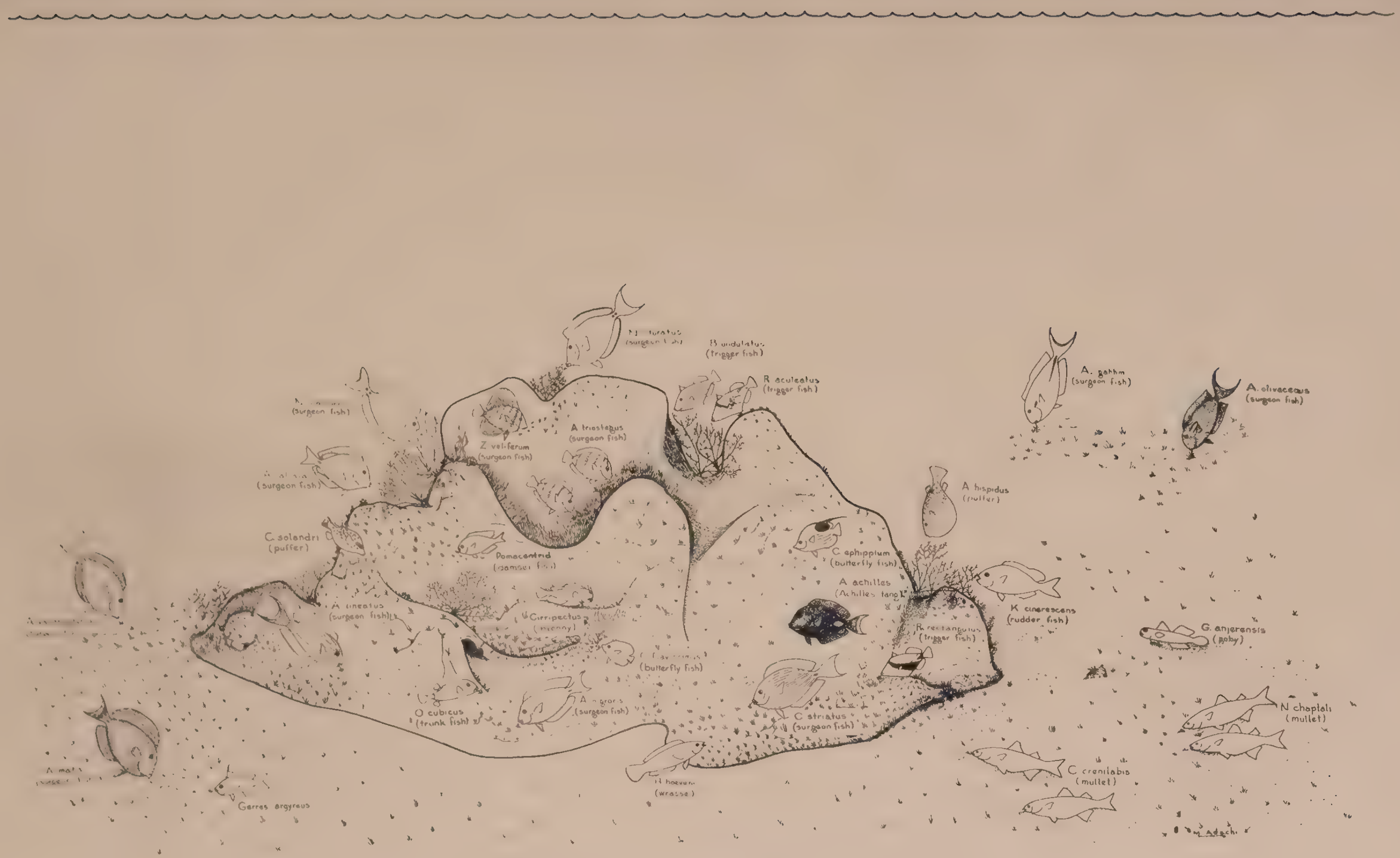
B undulatus
(trigger fish)
R aculeatus
(trigger fish)
(surgeon fish)
(surgeon fish)
A triostegus
(surgeon fish)
Z veliferum
(surgeon fish)
(surgeon fish)
C. solandri
(puffer)
Pomacentrid
(damsel fish)
A lineatus
(surgeon fish)
Cirripectus
(blenny)
(butterfly fish)
O cubicus
(trunk fish)
(surgeon fish)
(wrasse)
Gerres argyreus
A. gahhm
(surgeon fish)
A. olivaceous
(surgeon fish)
A hispidus
(puffer)
C ephippium
(butterfly fish)
A achilles
(Achilles tang)
K cinerescens
(rudder fish)
R rectangulus
(trigger fish)
G. anjerensis
(goby)
C striatus
(surgeon fish)
N chaptali
(mullet)
C crenilabis
(mullet)
M Adachi

FIG. 5. Herbivorous fish in characteristic feeding attitudes.

FISH FAUNA ASSOCIATED WITH RAMOSE CORALS AND THEIR DEAD BASES

An abundant fauna and flora are associated with branching or ramose types of coral heads. Not only is the coral head itself (polyps and contained zooxanthellae together with the filamentous algae living in the skeleton) almost a wholly contained ecological unit as stated by Odum & Odum (1955), but if we include the animal populations intimately associated with a branching head, it is even more complete as a contained ecological unit, and would justify community status by itself. Aside from the coral tissues themselves, there are among the fish associated with a single ramose head herbivores, carnivores, and omnivores. When we include the plethora of invertebrate types the community becomes more complex and complete. No doubt, a careful study of the microflora would reveal that it contains an adequate population of reducers too!

We have depicted the more important life about two types of ramose corals in Fig. 8. Comparatively few organisms are found in the interstices of the pedestal colonies of ramose corals because of their more exposed aspect. However, a number of species take refuge beneath the explanate head, and a large number of coral polyp feeders find such heads attractive because the branchlets are easily broken off, and, for some species, the terminal polyps are especially vulnerable for cropping.

In the ramose and cespitose heads with long branches, the interstices are attractive places of refuge for small crabs, shrimps, polychaetes, clams, and fishes. A number of highly carnivorous fish live within the interstices (*Gobiodon* spp., *Paragobiodon* spp., *Caracanthus* spp.) and do not venture outside the head. Other fishes such as the damsel fishes, *Dascyllus aruanus*, *Chromis caeruleus*, and *C. atripectoralis*, use the interstices only for protection, and swarm about just outside the head feeding on the abundant plankters. A number of carnivores such as the wrasses, *Gomphosus varius*, and *Epibulus insidiator*, and the butterfly fish, *Forcipiger longirostris*, have snouts either highly protractile or very elongate for probing deeply into the interstices in search of prey. Other wrasses constantly poke about amongst the branches searching for small crustaceans within reach.

On the bases of most of these heads algal filaments grow as a thin veneer. A number of herbivorous and omnivorous species graze and browse this material.

The following species are important members of the community of organisms associated with ramose coral heads:

Herbivores

Family Chaetodontidae (butterfly fishes)—*C. reticulatus*, *C. flavissimus;* Family Pomacentridae (damsel fishes)—*A. dicki.*

Carnivores

Family Muraenidae (moray eels)—*U. xanthopterus*, *E. marshallensis*, *G. buroensis*, *G. margaritophorus*, *G. fimbriatus;* Family Holocentridae (squirrel fishes)—*H. sammara*, *H. microstomus*, *H. laevis*, *H. diadema*, *H. spinifer;* Family Syngnathidae (pipefishes)—*C. i. waitei*, *C. f. conspicillatus;* Family Apogonidae (cardinal fishes)—*A. novemfasciatus*, *A. snyderi*, *A. exostigma*, *A. nigrofasciatus*, *A. novaeguineae*, *A. erythrinus*, *G. philippinus*, *P. quinquelineata;* Family Serranidae (groupers)—*C. urodelus;* Family Pseudochromidae—*P. melas*, *P. polyacantha*, *P. tapeinosoma;* Family Pempheridae (sweepers)—*P. oualensis;* Family Lutjanidae (snappers)—*S. cancellatus; Family Cirrhitidae* (hawkfish)—*A. arcatus*, *P. forsteri*, *C. aprinus*, *C. pinnulatus;* Family Scorpaenidae (scorpion fishes)—*S. parvipinnis;* Family Caracanthidae—*C. unipinnus;* Family Pomacentridae (damsel fishes)—*C. caeruleus*, *C. atripectoralis;* Family Labridae (wrasses)—*G. varius*, *C. oxycephalus*, *T. hardwickei*, *T. quinquevittata*, *E. insidiator*, *H. margaritaceus*, *N. taeniourus;* Family Gobiidae (gobies)—*G. rivulatus*, *G. erythrospilus*, *P. echinocephalus;* Family Balistidae (trigger fish)—*B. viridescens;* Family Monacanthidae (file fishes)—*O. longirostris;* Family Tetraodontidae (puffers)—*A. nigropunctatus*, *A. meleagris.*

Omnivores

Family Chaetodontidae (butterfly fishes)—*C. citrinellus*, *C. auriga;* Family Pomacentridae (damsel fish)—*D. aruanus;* Family Labridae (wrasses)—*T. lutescens*, *S. axillaris;* Family Balistidae (trigger fish)—*R. aculeatus*, *B. undulatus;* Family Monacanthidae (file fish)—*A. carolae;* Family Tetraodontidae (puffers)—*A. hispidus;* Family Canthigasteridae (sharp-backed puffers)—*C. solandri.*

TROPHIC LEVELS

One of the prime objectives of this study was to determine to which trophic levels the more important fish species belonged. Moreover, among reef ecologists there has always been some question as to reasons why such an apparently large fish population could exist when the primary producers in evidence seemed to be far less abundant than they should be on theoretical grounds, as interpreted from a pyramid of biomass based on the standing crop. This latter question has been solved to a great extent at least by the brilliant research of Odum & Odum (1955) on Eniwetok reefs. There they found that in the living coral heads themselves the zooxanthellae contained in the tissues of polyps and, even more important, the filamentous algae growing in the pores of the inert skeleton in bands below the outer living animal tissue, actually made the coral head more plant than animal, i.e., more producer than consumer, by a ratio of about 3 to 1. In addition to the algae contained in coral heads, there is considerable filamentous algae in the sand, shingle or rubble, dead coral heads, and the porous reef floor, as well, of course, as in the algal mats and seaweed visible to the naked eye. As Odum & Odum (1955) point out, "From the standpoint of the entire reef ecosystem it does not matter how much food made by algae within the live coral head [or within porous rock, rubble, and sand] is used by coral animals [or other animals] directly. Only by considering the large amount of producer tissue in [these subsurface locations] it is possible to explain the great preponderance of organisms classed as animals."

The second important consideration in the balance sheet of the coral reef ecosystem is the fact that most of the fish protoplasm visible to a swimmer represents herbivorous types belonging to the second trophic level. Moreover, on a more quantitative basis, although admittedly rough, Odum & Odum (1955) found that among the fishes there was a striking predominance on a weight

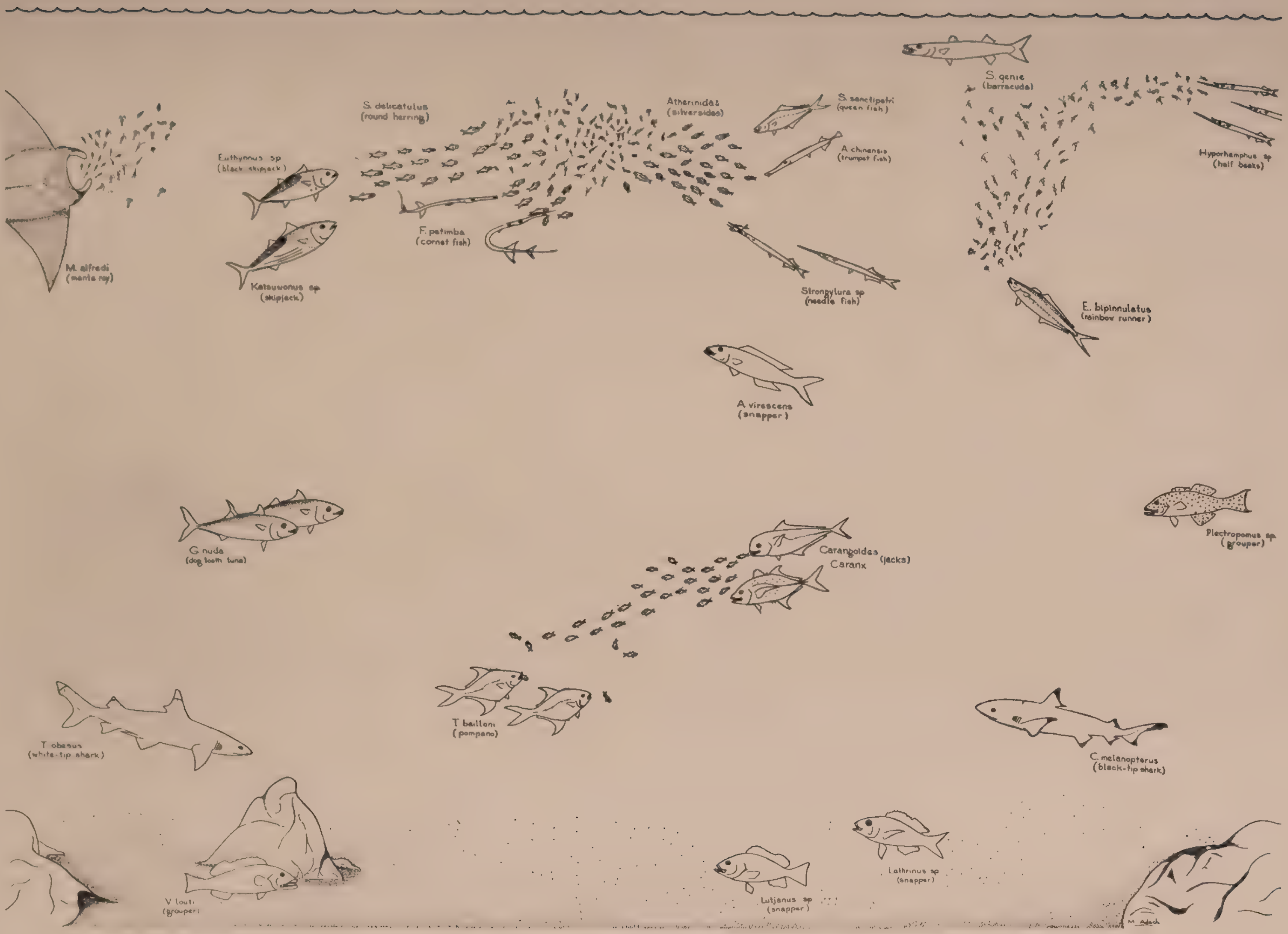
S. genie
(barracuda)
Hyporhamphus sp
(half beaks)
S. delicatulus
(round herring)
Atherinidae
(silversides)
S. sanctipetri
(queen fish)
A. chinensis
(trumpet fish)
Euthynnus sp
(black skipjack)
Katsuwonus sp
(skipjack)
M. alfredi
(manta ray)
F. petimba
(cornet fish)
Strongylura sp
(needle fish)
E. bipinnulatus
(rainbow runner)
A. virescens
(snapper)
G. nuda
(dog tooth tuna)
Carangoides
Caranx
(jacks)
Plectropomus sp
(grouper)
T. baillon
(pompano)
T. obesus
(white-tip shark)
C. melanopterus
(black-tip shark)
V. louti
(grouper)
Lutjanus sp
(snapper)
Lethrinus sp
(snapper)

FIG. 6. The mid-water and surface community.

basis of herbivorous parrot fishes, surgeon fishes, damsel fishes, and butterfly fishes in comparison to the wrasses, groupers, and other carnivores. The energetics of the system at this level are the most favorable in the entire food chain, regardless of the actual quantitative efficiency, since the herbivores are dependent upon the primary producers which, as in other ecosystems, have a much greater biomass than the carnivorous levels toward the apex of the pyramid.

Phylogenetically, certain interesting situations appear which are noteworthy. Our studies indicate that the more advanced and specialized fishes appear to be heading morphologically and physiologically toward the lower trophic levels where the stored energy in terms of food supply is in greater quantity. Note, for example, the foraging habits of the trigger fish (Balistidae), puffers (Tetraodontidae), etc., which have become omnivorous and frequently make entire meals on algae as well as on many little used invertebrates such as the sponges, coelenterates, echinoderms, and tunicates. Conversely, the most primitive fishes in the phylogenetic scale are exclusively carnivores, and usually so at the fourth or fifth trophic levels where comparatively little food is available. The more generalized species appear to fall mostly in the third and fourth trophic levels where a considerable amount of comparatively easy to get food items is available to them in the form of invertebrates or small fishes of the second and third trophic levels. The invertebrates comprise the greatest biomass of the second trophic level (Odum & Odum, 1955), and, although their detailed food habits are not accurately known, we are able to assign them arbitrarily to the second trophic level for the most part, although some comprise a portion of the third trophic level.

The fish families which comprise the bulk of the biomass at the second trophic level, surgeon fishes (Acanthuridae), damsel fishes (Pomacentridae), and rabbit fishes (Siganidae) are rather highly evolved, specialized fishes also. The dental and other morphological modifications and physiological changes from the more primitive type fish are considerable, and these did not evolve in spite of the great mass of plant food available until comparatively lately as regards the evolutionary time scale of the group. It is still an enigma why the biomass of herbivorous fishes is so proportionately great on tropical reefs where larger seaweeds are not abundantly available, and so proportionately small along coastal shores in the temperate and arctic seas.

At the present time research on the primary producers of coral reef ecosystems in the Marshall Islands has reached a comparatively high level of understanding. The present studies should provide the framework for far greater knowledge at the higher trophic levels for the higher organisms, but there still remains to be known the role of the myriads of invertebrates which inhabit the reefs.

Below are listed the species comprising the several trophic levels on Marshallese reefs. It should be borne in mind that the trophic level into which a particular carnivore is placed frequently depends upon its growth stage. Many juvenile carnivores occupy a trophic level one or two levels below that eventually occupied as an adult. These changes have been taken into consideration when borne out by our analysis of their food and feeding habits.

First Trophic Level (Primary Producers)

Algae

Second Trophic Level (Primary Consumers; Herbivores)

Family Mugilidae (mullets)—*Crenimugil crenilabis, Neomyxus chaptali;* Family Leiognathidae (silver perch)—*Gerres argyreus;* Family Siganidae (rabbit fishes)—*Siganus rostratus;* Family Kyphosidae (pilot fish)—*Kyphosus cinerascens;* Family Chaetodontidae (butterfly fishes)—*Chaetodon auriga, C. ephippium, C. reticulatus, Centropyge flavissimus;* Family Acanthuridae (surgeon fishes)—*Acanthurus achilles, A. aliala, A. nigroris, A. xanthopterus, A. guttatus, A. lineatus, A. mata, A. gahhm, A. olivaceus, A. t. triostegus, Ctenochaetus striatus, Naso lituratus, N. unicornis, Zebrasoma veliferum;* Family Pomacentridae (damsel fishes)—*Abudefduf amabilis, A. biocellatus, A. dicki, A. glaucus, A. lacrymatus, A. leucopomus, A. saxatilis, A. septemfasciatus, A. sordidus, Dascyllus aruanus, Pomacentrus albofasciatus, P. jenkinsi, P. nigricans, P. vaiuli;* Family Labridae (wrasses)—*Halichoeres hoeveni;* Family Blenniidae (blennies)—*Cirripectus sebae, C. variolosus, Exallias brevis, Istiblennius coronatus, I. paulus;* Family Balistidae (trigger fishes)—*Balistapus undulatus, Melichthys vidua, Rhinecanthus aculeatus, R. rectangulus;* Family Monacanthidae (file fishes)—*Amanses carolae;* Family Ostracionidae (trunk fishes)—*Ostracion cubicus;* Family Tetraodontidae (puffers)—*Arothron hispidus;* Family Canthigasteridae (sharp-backed puffers)—*Canthigaster solandri.*

Third Trophic Level (Secondary Consumers; Carnivores)

Family Mobulidae (manta rays)—*Manta alfredi;* Family Dussumieridae (round herrings)—*Spratelloides delicatulus;* Family Clupeidae (sardines)—*Harengula kunzei;* Family Ophichthidae (snake eels)—*Brachysomophis sauropsis;* Family Muraenidae (moray eels)—*Echidna leucotaenia, E. polyzona, E. zebra, Gymnothorax buroensis, G. flavimarginatus, G. javanicus, G. margaritophorus, G. petelli, Rabula marshallensis, Uropterygius xanthopterus;* Family Congridae (conger eels)—*Conger noordzieki;* Family Moringuidae (whip eels)—*Moringua macrochir;* Family Synodontidae (lizard fish)—*Synodus variegatus;* Family Hemiramphidae (half-beaks)—*Hyporhamphus affinis, H. laticeps;* Family Bothidae (flounders)—*Bothus mancus;* Family Holocentridae (squirrel fishes)—*Holocentrus diadema, H. lacteoguttatus, Holocentrus laevis, H. microstomus, H. spinifer, Myripristis berndti, M. microphthalmus;* Family Syngnathidae (pipefishes)—*Corythoichthys flavofasciatus conspicillatus, C. intestinalis waitei;* Family Atherinidae (silversides)—*Pranesus pinguis, Allanetta ovalaua, Stenatherina temmincki;* Family Polynemidae (threadfins)—*Polydactylus sexfilis;* Family Carangidae (jacks) *Elagatis bipinnulatus, Trachurops crumenophthalmus;* Family Apogonidae (cardinal fishes)—*Apogon erythrinus, A. exostigma, A. nigrofasciatus, A. novaeguineae, A. snyderi, Cheilodipterus macrodon, Gymnapogon philippinus;* Family Serranidae (groupers)—*Cephalopholis argus, C. urodelus, Epinephelus hexagonatus, E. macrospilos, E. merra, E. spilotus, Variola louti;* Family Pseudochromidae—*Plesiops melas, P. nigricans, Pseudochromis tapeinosoma, Pseudogramma polyacantha;* Family Pempheridae (sweepers)—*Pempheris oualensis;* Family Lutjanidae (snappers)—*Gnathodentex aureolineatus, Gymnocranius griseus, Lutjanus gibbus, L. vaigiensis, L. vitta, Scolopsis cancellatus;* Family Leiognathidae (silver perch)—*Gerres argyreus;* Family

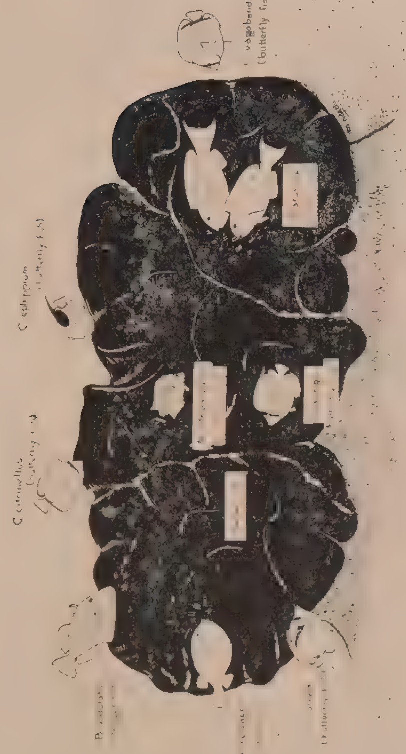
vagabundus
(butterfly fish)
C. ephippium
(butterfly fish)
C. citrinellus
(butterfly fish)

FIG. 7. Feeders upon glomerate corals.

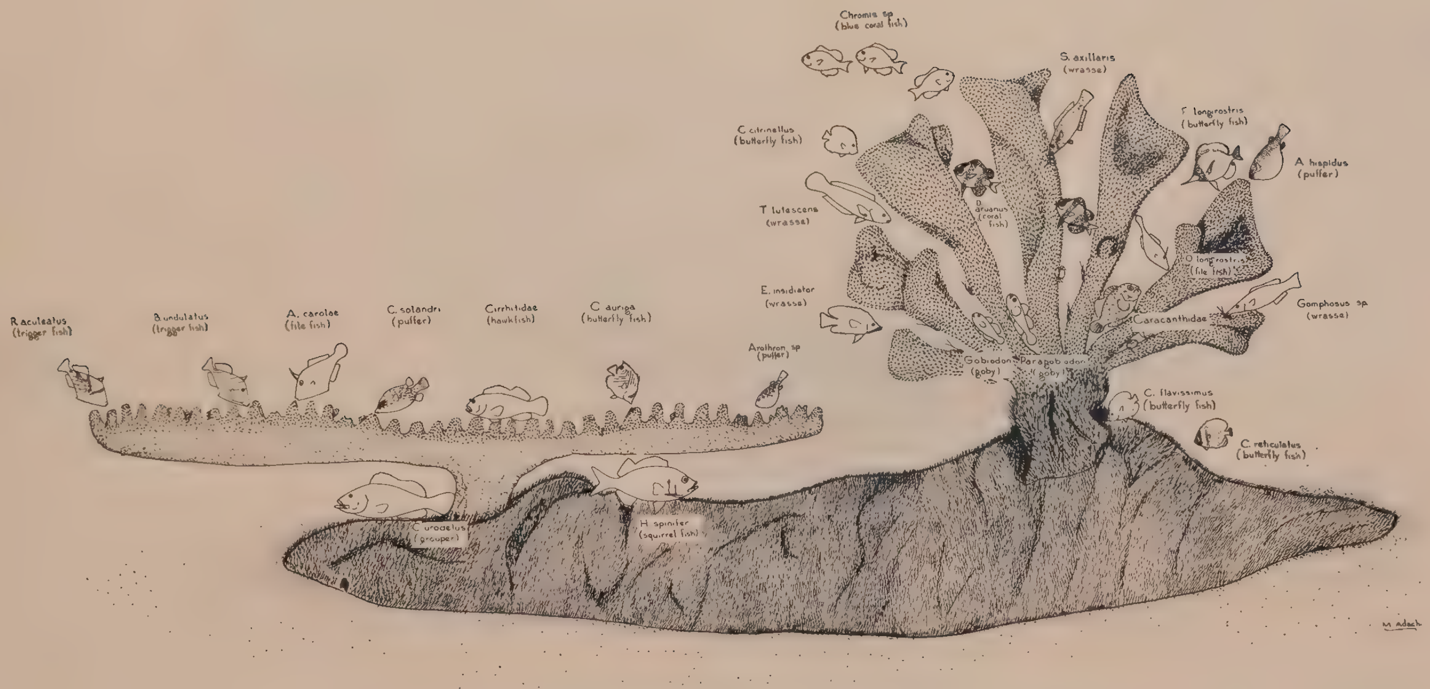
Chromis sp
(blue coral fish)
S. axillaris
(wrasse)
F. longirostris
(butterfly fish)
A. hispidus
(puffer)
C. citrinellus
(butterfly fish)
D. aruanus
(coral fish)
T. lutescens
(wrasse)
O. longirostris
(file fish)
E. insidiator
(wrasse)
Gomphosus sp
(wrasse)
Caracanthidae
Arothron sp
(puffer)
Gobiodon
(goby)
Paragobiodon
(goby)
C. flavissimus
(butterfly fish)
C. reticulatus
(butterfly fish)
R. aculeatus
(trigger fish)
B. undulatus
(trigger fish)
A. carolae
(file fish)
C. solandri
(puffer)
Cirrhitidae
(hawkfish)
C. auriga
(butterfly fish)
C. urodelus
(grouper)
H. spinifer
(squirrel fish)
M. Adach

FIG. 8. Fishes associated with ramose corals.

Sparidae (snappers)—*Monotaxis grandoculis*; Family Mullidae (goat fishes)—*Mulloidichthys samoensis, Parupeneus barberinus, P. trifasciatus, Upeneus arge*; Family Cirrhitidae (hawkfish)—*Amblycirrhitus arcatus, Cirrhitichthys aprinus, Cirrhitus pinnulatus*; Family Chaetodontidae (butterfly fishes)—*Chaetodon auriga*; Family Scorpaenidae (scorpion fish)—*Pterois radiata, P. volitans, Scorpaenodes parvipinnis*; Family Caracanthidae—*Caracanthus unipinnus*; Family Platycephalidae (flatheads)—*Thysanophrys* sp.; Family Pomacentridae (damsel fish)—*Abudefduf glaucus, A. lacrymatus, A. leucopomus, A. saxatilis, A. septemfasciatus, A. sordidus, Dascyllus aruanus, Chromis atripectoralis, C. caeruleus, Pomocentrus pavo*; Family Labridae (wrasses)—*Cheilinus chlorourus, C. oxycephalus, C. trilobatus, Coris angulata, C. gaimardi, Epibulus insidiator, Gomphosus varius, Halichoeres hoeveni, H. hortulanus, H. margaritaceus, H. marginatus, H. trimaculatus, Hemigymnus melapterus, Labroides dimidiatus, Macropharyngodon meleagris, M. pardalis, Novaculichthys taeniourus, Pseudocheilinus hexataenia, Stethojulis axillaris, Stethojulis* sp., *Thalassoma hardwickei, T. lucasanum marnae, T. lutescens, T. quinquevittata, T. umbrostygma*; Family Gobiidae (gobies)—*Bathygobius f. fuscus, Gnatholepis anjerensis, Gobiodon rivulatus, G. erythrospilus, Gobius ornatus, Paragobiodon echinocephalus*; Family Eleotridae (sleepers)—*Valenciennea strigata, V. violifera*; Family Microdesmidae—*Paragobioides grandoculis*; Family Parapercidae (sand perch)—*Parapercis cephalopunctatus, P. clathrata*; Family Blenniidae (blennies)—*Cirripectus sebae, Istiblennius paulus*; Family Brotulidae—*Dinematichthys iluocoeteoides*; Family Balistidae (trigger fish)—*Balistapus undulatus, Pseudobalistes flavimarginatus, P. fuscus, Rhinecanthus aculeatus, R. rectangulus*; Family Ostracionidae (trunk fishes)—*Ostracion cubicus*; Family Tetraodontidae (puffers)—*Arothron hispidus, A. mappa*; Family Diodontidae (spiny puffers)—*Diodon hystrix*.

Fourth Trophic Level (Tertiary Consumers; Carnivores)

Family Carcharhinidae (gray sharks)—*Carcharhinus melanopterus, C. menisorrah*; Family Triakidae (smooth dogfishes)—*Triaenodon obesus*; Family Muraenidae (moray eels)—*Gymnothorax javanicus, G. flavimarginatus, G. undulatus*; Family Synodontidae (lizard fishes)—*Synodus variegatus, Saurida gracilis*; Family Belonidae (needle fishes)—*Strongylura incisa, S. gigantea*; Family Hemiramphidae (half-beaks)—*Hyporhamphus laticeps*; Family Bothidae (flounders)—*Bothus mancus*; Family Holocentridae (squirrel fishes)—*Holocentrus microstomus*; Family Aulostomidae (trumpet fishes)—*Aulostomus chinensis*; Family Fistulariidae (cornet fishes)—*Fistularia petimba*; Family Carangidae (jacks)—*Trachinotus bailloni, Carangoides ferdau jordani, Caranx melampygus*; Family Apogonidae (cardinal fishes)—*Apogon novemfasciatus, Paramia quinquelineata*; Family Priacanthidae (big eyes)—*Priacanthus cruentatus*; Family Serranidae (groupers)—*Epinephelus merra, E. fuscoguttatus, E. kohleri, E. hexagonatus, E. macrospilos, E. spilotus, Variola louti, Cephalopholis argus, Anyperodon leucogrammicus, Plectropomus truncatus*; Family Pseudochromidae—*Plesiops melas*; Family Pempheridae (sweepers)—*Pempheris oualensis*; Family Lutjanidae (snappers)—*Lutjanus monostigmus, L. bohar, L. vitta, L. gibbus, Lethrinus microdon*; Family Mullidae (goat fishes)—*Parupeneus cyclostomus*; Family Cirrhitidae (hawkfishes)—*Paracirrhites forsteri*; Family Chaetodontidae (butterfly fishes)—*Chaetodon vaga-*

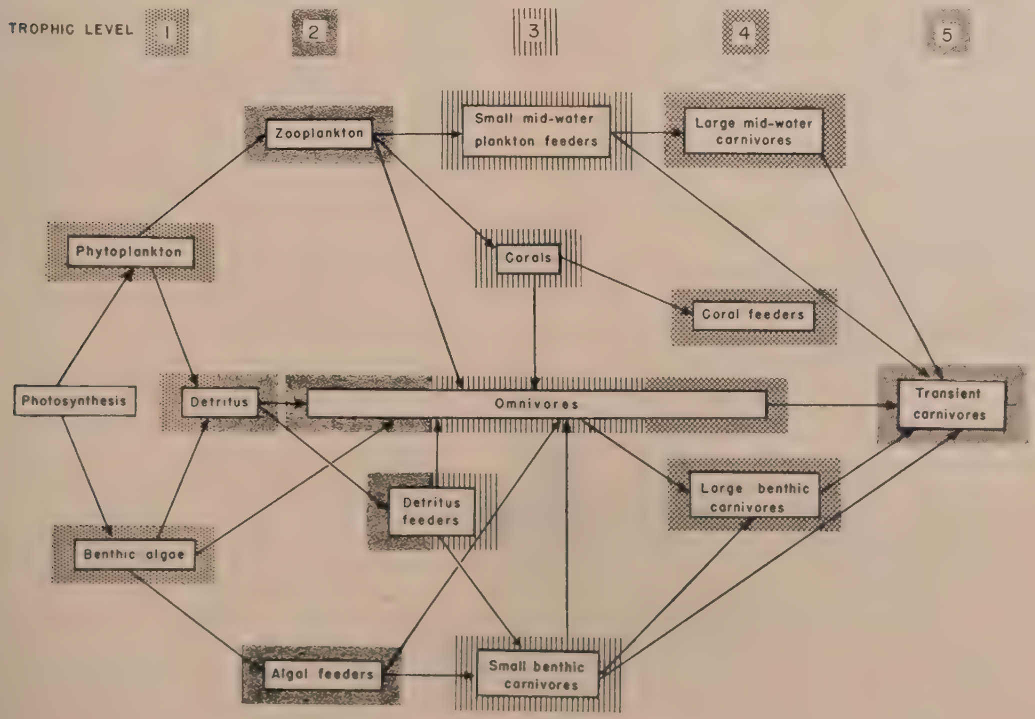

FIG. 9. The food web of Marshallese reefs.

bundus, C. ephippium, C. citrinellus, C. auriga, C. lunula, Megaprotodon strigangulus; Family Scorpaenidae (scorpion fishes)—*Scorpaenopsis gibbosa, Synanceja verrucosa;* Family Scaridae (parrot fishes)—*Cryptotomus spinidens, Scarus sordidus, S. bicolor;* Family Parapercidae (sand perches)—*Parapercis cephalopunctatus, P. clathrata;* Family Blenniidae (blennies)—*Aspidontus taeniatus;* Family *Balistidae* (trigger fishes)—*Balistoides viridescens, Balistapus undulatus;* Family Monacanthidae (file fishes)—*Amanses carolae, Oxymonacanthus longirostris;* Family Tetraodontidae (puffers)—*Arothron nigropunctatus, A. meleagris, A. hispidus, Arothron* sp.

Fifth Trophic Level

(Quaternary Consumers; Roving Carnivores)

Family Carcharhinidae (gray sharks)—*Carcharhinus melanopterus, C. menisorrah;* Family Triakidae (smooth dogfishes)—*Triaenodon obesus;* Family Sphyraenidae (barracudas)—*Sphyraena qenie;* Family Scombridae (tunas)—*Gymnosarda nuda, Katsuwonus pelamis, Euthynnus affinis yaito.*

THE FOOD WEB

Figure 9 depicts in summarized form an overall picture of Marshallese food chains. For the sake of brevity various foraging activities have been combined under inclusive categories such as "algal feeders," etc. The reader is referred to earlier portions of the text for the specific constituents of these generalized categories. It is to be noted that only the major food pathways are shown in this food web, this being done for simplicity's sake because of the large number of species studied.

SUMMARY

1. Major gaps in our knowledge of coral reef ecology lie in our understanding of the taxonomic composition of the reef biota, the nature of biotic interaction between various trophic levels, and the specific community relationships obtaining in the several physiographic areas of a coral reef.

2. The present study attempts to fill these gaps by reporting upon the food, feeding habits, and ecological relationships of Marshallese fishes. The study was conducted at Bikini, Arno, and Eniwetok Atolls during the period 1947-1955. The geographical and physical aspects of these three atolls are described in detail along with descriptions of the various types of reefs encountered at each.

3. Fish examined for this study were obtained primarily by rotenone poisoning, with supplementary techniques (spears, hook and line, explosives) being used when warranted. Data recorded for each specimen were: standard length, sex, gonadal development, nature of alimentary tract, dentition, and type of food ingested. Over 2,000 individual stomachs were examined for the food study, and supplementing the laboratory work were hundreds of hours of underwater observation. We believe that combining the laboratory studies with the field observations enables us to present natural interpretations for the various ecological situations studied.

4. A discussion of food and feeding habits is presented for 56 families, 127 genera, and 233 species of Marshallese fishes, these figures representing more than half of the genera and somewhat less than half of the species known from the area. In addition to a discussion of each species, there are summaries by family and occasionally by genus.

5. The feeding habits of the species examined are categorized by foraging method as follows: algal feeders (consumers of unicellular algae, grazers, browsers, incidental algal feeders), detritus feeders, scavengers, zooplankton feeders, carnivores (feeders on fossorial, benthonic, and mid-water fauna, resident and transient roving carnivores), coral polyp feeders (browsers, grazers, and feeders on branching coral tips), and omnivores (facultative and incidental). Items frequently regarded as inedible (corals, echinoderms, sponges) were found to constitute significant portions of the diets of several fish groups.

6. The characteristic associations between fish and various coral reef habitats are illustrated and described for the following situations: supra- and intertidal pools, seaward reef flat, surf zone and surge channels, rocky and compacted sand substrates bearing algae, ledges and caverns, mid-water and surface communities, and glomerate and ramose coral heads and their bases.

7. The fishes considered are assigned to trophic levels as follows: primary consumers (herbivores), secondary and tertiary consumers (carnivores), and quaternary consumers (roving carnivores). Herbivorous species dominate Marshallese reefs because of favorable energetics between them and the great primary producer reef biomass. The more advanced fishes (trigger fish, puffers, surgeon fish, etc.) are typically members of the lower trophic levels, whereas the more primitive forms are carnivorous and frequently rank at the highest trophic levels.

8. A food web depicting energy flow in a coral reef ecosystem is presented.

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Reprinted from SCIENCE, May 20, 1960, Vol. 131, No. 3412, page 1532

Uptake of Glucose from Solution by the Solitary Coral, Fungia

Abstract. The removal of glucose from solution in sea water by the coral, *Fungia*, has been followed with D-glucose-C^{14}. From 15 to 37 percent of the sugar in 200 ml of solution is taken up per hour from concentrations of 1 to 40 mg/liter. This rate of uptake provides sufficient material to account for the maintenance metabolism of the coral at sugar concentrations of 3.75 to 7.25 mg/liter.

The observations to be reported were made using D-glucose-C^{14} added to the sea water in which individual corals were maintained. The concentration of labeled material was estimated at suitable intervals by evaporating 0.5 ml samples on planchets and counting with a thin-window Geiger tube. Each determination was made in quintuplicate. Although self-absorption in dried sea water samples is considerable, dilution curves indicated a linear relation between the counting rate and the concentration of labeled glucose.

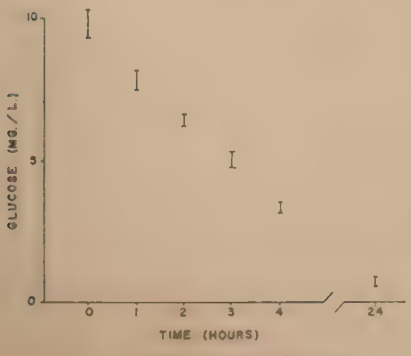

Fig. 1. Disappearance of sugar.

Fig. 1 illustrates the disappearance of added sugar in a typical set of observations. The volume of the solution was 200 ml. Uptake occurred in the same fashion in the presence of streptomycin (50 mg/liter). The rate of disappearance in darkness was comparable to that observed in diffuse sunlight. The radioactivity in 200 ml of solution maintained as a blank did not change over a 24 hour period.

The radioactive carbon which disappears from solution during a 4 hour period can be recovered in a sodium hydroxide digest of the animal. After 24 hours, a portion of the C^{14} remaining in the sea water diffuses from an acid to a base medium in a diffusion chamber, suggesting the presence of $C^{14}O_2$. Thus *Fungia* is apparently capable of removing glucose from solution at low concentrations and using it as a source of energy.

Table 1 lists the observed rate of uptake at various initial concentrations of glucose. The volume in each case is 200 ml of solution. A concentration of 1 mg/liter probably does not represent a lower limit for effective uptake but is rather a limit imposed by the specific activity of the labeled sugar. At this concentration, the observed rate was 5.3 ± 0.68 count/min.

It is of interest to consider whether this process is potentially significant as a source of nutrients for the animal. Animals were kept in darkness, and oxygen consumption was determined by the Winkler method. Individuals ranged in wet weight from 21.4 to 48.0 gm, and oxygen consumption ranged from 0.11 to 0.22 ml per individual per hour at a temperature of 26°C (0.047 ± 0.015 ml/gm hr). These figures imply that the equivalent of 0.15 to 0.29 mg of carbohydrate per hour must be acquired by an individual to support maintenance metabolism.

From the observations presented in Table 1, we may assume a rate of removal of 20 percent per hour for the carbohydrate present in 200 ml of sea water. An ambient concentration of 3.75 to 7.25 mg/liter is thus sufficient to account for the observed oxygen consumption. No figures are available for naturally occurring concentrations of carbohydrate for waters near Oahu. Lewis and Rakestraw (*1*) reported concentrations of an unidentified carbohydrate as high as 7.9 mg/liter in filtered sea water samples from coastal lagoons near San Diego. Their determinations for more open waters are considerably lower.

Table 1. Removal of glucose from sea water by *Fungia*.

Initial concn. of glucose (mg/liter)	Amount removed in first hour (%)	Amount removed (mg)
1.0	15*	0.03
1.0	28*	.06
1.0	25*	.05
1.0	20*	.04
4.0	29	.23
4.0	31	.25
4.0	37	.30
4.0	25	.20
10.0	30	.60
10.0	16	.32
10.0	23	.46
10.0	22	.44
40.0	16	1.28
40.0	22	1.46

* Calculated from determinations after 2 hours.

Values reported for total dissolved organic material (*2*, *3*) are approximately 5 mg/liter for open water. Unfortunately, our information concerning the character of this dissolved organic material is modest (*4*). However, we need not limit our speculations to the carbohydrate fraction of this material since many invertebrates are capable of removing amino acids from dilute solution (*5*, *6*). Unpublished observations indicate that this is also true of *Fungia*.

If we assume that the naturally occurring carbohydrate in sea water is utilizable and is taken up at the rate observed for glucose, *Fungia* can obtain sufficient material to account for maintenance metabolism in selected locations. If we make similar assumptions concerning all the dissolved organic material, a favorable location need not be stipulated. Information to support these assumptions is not available. However, the hypothesis that dissolved organic material may provide a significant fraction of the food of aquatic animals deserves further investigation (*7*).

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7 March 1960

Int. Revue ges. Hydrobiol. | 45 | 2 | 1960 | 175—196

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THE FUNCTIONAL MORPHOLOGY OF *CYPRAEA CAPUTSERPENTIS* L. AND AN INTERPRETATION OF THE RELATIONSHIPS AMONG THE CYPRAEACEA

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I. INTRODUCTION

The Cypraeacea are generally regarded as carnivorous gastropods which feed on sessile tunicates and coelenterates (Vayssière 1923, 1927; Graham 1954). The anatomy and mode of life of the Triviinae (*Trivia* and *Erato*) and Amphiperasiinae (*Simnia*) of British waters have been well described by Graham (1949, 1954) and Fretter (1946, 1951), and the life history by Lebour (1932, 1933a, 1933b, 1935). The biology and anatomy of the Cypraeinae (*Cypraea*), the majority of which occur in tropical waters are less well known. A recent reference to the biology of *Cypraea* describing some species as primary herbivores on coral reefs of the Pacific (Odum 1955) is in contrast to earlier descriptions of the Cypraeinae as carnivores feeding on corals and sponges (Vayssière 1923, 1927; Rau 1934). Apart from the comprehensive descriptions of the nervous system by Bouvier (1887) and Rilse (1931), which include descriptions of the diffuse pedal nerve cords, accounts of the anatomy are fragmentary and suggest some puzzling features from the standpoint of functional morphology. The anterior portion of the digestive system includes a crop or "jabot" (Amaudrut 1898, Risbec 1937), and an open seminal groove has been described in the reproductive system of the males (Rau 1934). Consideration of the occurrence of these apparently archaic features in one subfamily of a group usually regarded as specialized among mesogastropods has been the stimulus for a detailed study of one species of the Cypraeinae, *Cypraea caputserpentis* L., and the relationships of the Cypraeinae to the members of the Cypraeacea are discussed in light of this investigation.

The names used are those of Thiele (1931) with the exception that all species of the Cypraeina are referred to the genus *Cypraea.*

II. FUNCTIONAL MORPHOLOGY OF *CYRAEA CAPUTSERPENTIS* L.

1. *Material and Methods*

Specimens of *C. caputserpentis* were collected in the Hawaiian Islands and dissected both alive and after preservation. Fixatives for histological preparations included Bouin's and Zenker's fluids and Flemming-without-acetic. Although Bouin's fluid was satisfactory for gross structure and most cellular detail, Flemming-without-acetic appeared to be a better fixative in general as tissues were less subject to distortion and details of glandular tissue were more concise when fixed in it. Paraffin sections were cut at eight and ten microns and stained with Mallory (Pantin technique), Heidenhain's iron haemato xylin (counterstained with eosin and fast green), and van Gieson's picro-fuchsin.

2. *Habitat*

C. caputserpentis is a widely distributed Indo-Pacific species, occurring from the East Coast of Africa to Hawaii. Its occurrence in general is associated with coral reefs. In Hawaii *C. caputserpentis* is eurytopic, occurring in areas where there is a hard substrate and sand studded with loose rocks and coral and a more or less luxuriant algal growth, from the low tide zone seaward to a depth of three meters. *C. caputserpentis* is nocturnal. During the day the animals are concealed under rocks and coral and in crevices where they may be distinguished by their highly polished brown and white shells. After dark the animals become active, crawling about in tidepools or on turf-covered benches covered by several inches of water.

3. *Foot and Mantle*

The mantle which covers the shell when the animals are active is olive-brown with green and yellow splashes visible in the ground color. Papillae projecting from the mantle are of two types: those nearest the foot are conical and those which are medial are dendritic. Most of the papillae are tipped with red. The siphon which protrudes from the anterior aperture of the shell is formed by a fan-like extension of the mantle, and is fringed with a single row of evenly spaced, short, conical projections. The proboscis projects anteriorly below the siphon, with the tentacles lateral to it. Well-developed eyes are located on lateral extensions at the base of the tentacles. The foot is dorso-laterally extensible and is slightly darker in color than the mantle. The sole is light gray, oval, bluntly rounded anteriorly and tapered posteriorly. A shallow groove channels the anterior end.

The glandular equipment of the foot appears to be associated with the dorsal epithelium only (fig. 1, *DEP*) and is similar in both males and females. A series of pores (*P*) on the dorso-lateral surfaces discharge strings of mucus when the animal is disturbed. The glands (*DG*) are simple acinous arrangements lying below the sparsely ciliated columnar cells of the dorsal epithelium. Secreting cells line the lumina and communicate with the exterior by the pores (*P*) which protrude between the epithelial cells. The nuclei of the secreting cells are excentric, lying

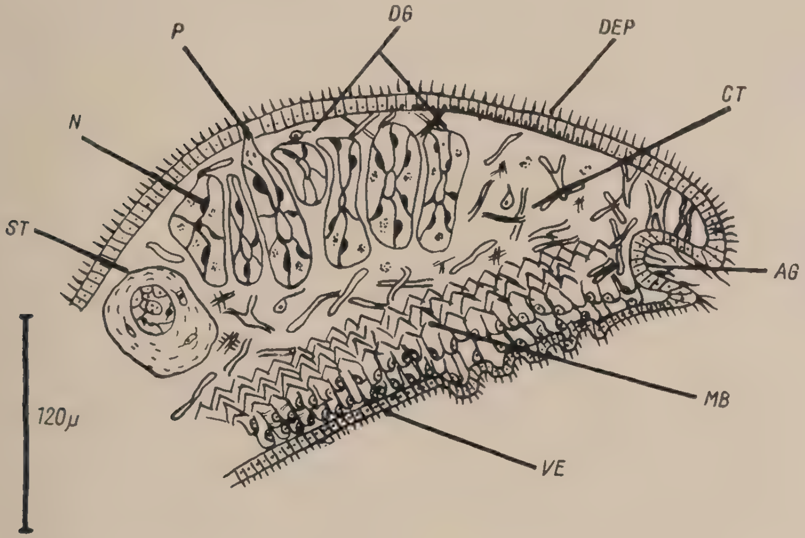

Fig. 1. *Cypraea caputserpentis.* Sagittal section through the foot showing the anterior channel and the pedal glands (from preparations with Zenker's fluid and eosin). *AG* anterior channel; *CT* connective tissue; *DEP* dorsal epithelium; *DG* dorsal glands; *MB* muscle bundles; *N* nucleus; *P* pores; *ST* otoliths; *VE* ventral epithelium.

against the cell membrane. No glandular cells appear to be associated with the anterior channel (*AG*), the epithelium of which consists of regular tall columnar cells bearing long cilia which beat toward the lateral edges of the groove. Below the dorsal glands connective tissue (*CT*) predominates, lightly staining fibers directed more or less ventrally and interspersed with a few spindleshaped muscle fibers. A layer of regularly arranged compact muscle bundles (*MB*) lies near the ventral epithelium (*VE*), which bears a brush-like ciliary border. Throughout the lenght of the foot the ganglia of the pedal nerve cords are visible toward the medial aspect. Closely associated with the ganglia are otoliths (*ST*), hollow vesicles containing two or three excentric, amorphous concretions. The vesicles are lined by ciliated epithelial cells.

The mantle cavity is that of a typical prosobranch, accomodating the ctenidium, osphradium, hypobranchial gland, pallial genital ducts, and, in the male, a large non-invaginable penis. The single, elongate, curved left ctenidium is attached to the roof of the mantle cavity for some two-thirds of its length, and encloses a trifid osphradium within its curvature. The large hypobranchial gland covers the posterior portion of the pallial roof between the ctenidium and rectum, its glandular epithelium folded with large pleats which are oriented dorso-ventrally.

4. *Feeding Habits and Digestive System*

a) Buccal Region

C. caputserpentis browses continuously over the substrate, rasping off fragments of algae and sponge, and incidentally procuring small crustacea, larval molluscs, and sand grains.

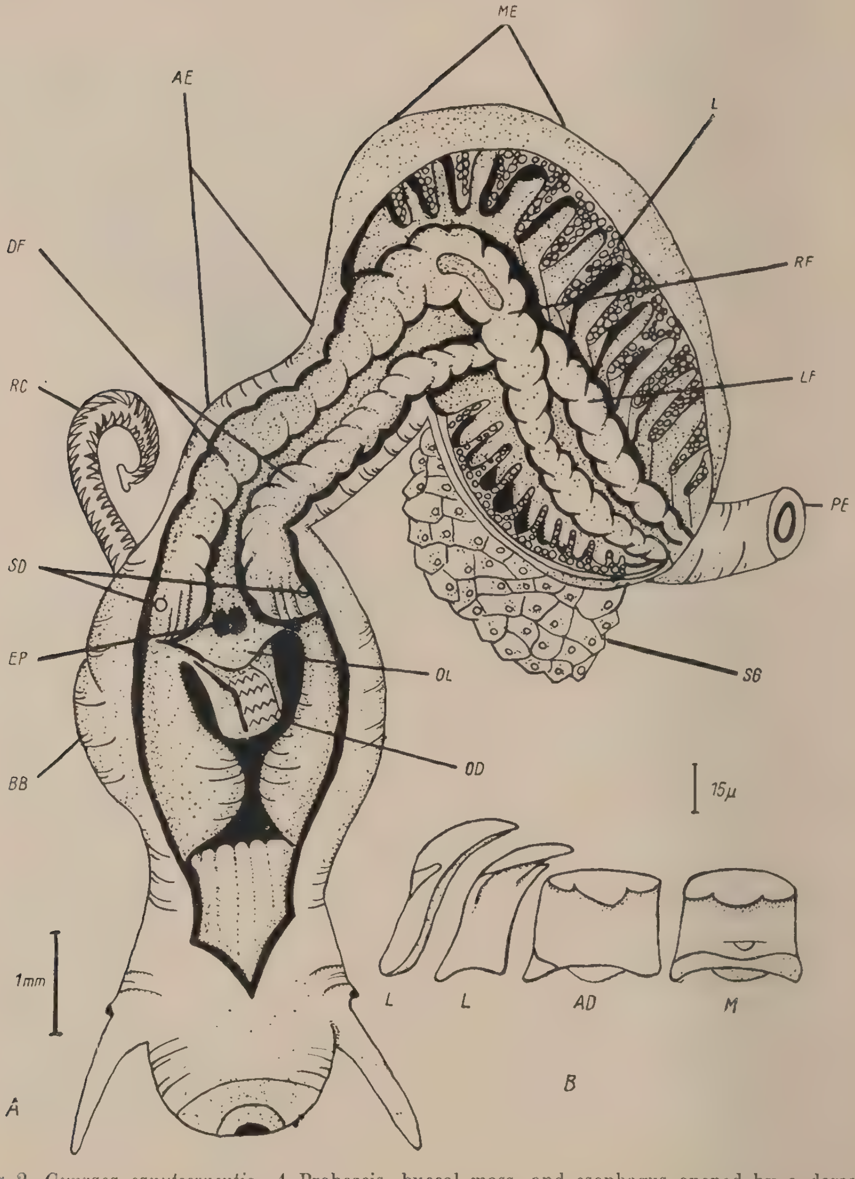

Fig. 2. *Cypraea caputserpentis*. *A* Proboscis, buccal mass, and esophagus opened by a dorsal incision; the odontophore pulled back to show the walls of the buccal cavity, the anterior esophagus straightened, and the salivary glands pulled laterally. *AE* anterior esophagus; *BB* buccal bulb; *DF* dorsal folds; *EP* esophageal pockets; *L* lamellae; *LF* left fold; *ME* mid-esophagus; *OD* odontophore; *OL* odontophoral lappet; *PE* posterior esophagus; *RC* radular caecum; *RF* right fold; *SD* ducts of salivary glands; *SG* salivary glands. B Half row of radular teeth. *L* laterals; *AD* admedians; *M* median.

The mouth lies at the summit of a short pleurembolic proboscis which is continuous posteriorly with the buccal bulb (fig. 2A, *BB*). The latter structure occupies the haemocoele of the head and inserted into it are the extensor and retractor muscles of the odontophore. The odontophore (*OD*), which bears the radular ribbon, covers the floor of the buccal cavity, the walls of which are smooth, projecting medially so that the cavity itself is a vertical cleft. Above the odontophore the food channel is a dorso-ventrally depressed duct bordered by a pair of folds (*DF*) which are macroscopically divided by longitudinal grooves and histologically lined by a ciliated columnar epithelium with occasional gland cells. The dorsal surface is composed of an epithelium of columnar cells bearing a mucous border. A triangular lappet (*OL*) originating laterally from the walls of the buccal cavity extends across the odontophore separating the radular caecum from the food channel and marking the posterior border of the buccal cavity. The ducts of the salivary glands (*SD*) open on either side of the odontophore.

The radula (fig. 2B) is of general taenioglossan arrangement with seven teeth in each row. The laterals (*L*) are concave blades, the inner wider than the outer and distinguished by a strong basal protrusion. The admedians (*AD*) and median (*M*) are tricuspid, small lateral cusps flanking the central cusp. That the individual teeth are not specialized in function is suggested both by the nature of the food and by observation of feeding tracks which indicate that the teeth are all simply raking and scraping tools.

b) Esophagus

Extending posteriorly from the buccal cavity, the anterior esophagus (fig. 2A, *AE*) curves sharply to the left and the esophagus and stomach lie to the left of the mid-line of the body. The folds of the food channel continue through the anterior esophagus, the folds dividing the lumen into dorsal and ventral chambers. Posteriorly the dorsal folds diminish in height and gradually shift toward the ventral floor, resulting in the disappearance of the ventral channel in the region of the nerve ring. The histology of the anterior esophagus is similar at first to that in the buccal cavity, but the columnar cells are gradually succeeded by cells which although ciliated are somewhat goblet-shaped and appear empty except for some conspicuous yellow granules in the basal portion when stained with Mallory (fig. 3A). The ventral channel is distinguished in its anterior portion by a pair of shallow depressions (fig. 2A, *EP*) immediately posterior to the odontophoral lappet. The depressions are histologically distinct from the other portions of the anterior esophagus, consisting of closely packed columnar cells with a homogeneous cytoplasm (fig. 3B). The nuclei stain red with Mallory and are located centrally in the basal portion of the cells. These depressions are variously developed in other species of *Cypraea*, forming long diverticula in *C. cinerea* Gmelin and *C. cervus* L. The single diverticulum illustrated by Amaudrut (1898) in *C. arabica* L. has not been noted in any species (including *C. arabica*) thus far examined.

Posterior to the nerve ring the esophagus expands into what has been termed the "jabot" or crop (Malard 1887; Vayssière 1923, 1927; Risbec 1937, 1955). This is a pyriform structure (fig. 2A, *ME*) over which lie the lobed salivary glands (*SG*). The food channel is similar to that in the anterior esophagus except that the morphologically right and left walls have exchanged places, the right wall crossing over the left and becoming the topographically left wall in the region of the nerve ring (*RF*, *LF*). Numerous ventrally projecting lamellae (*L*)

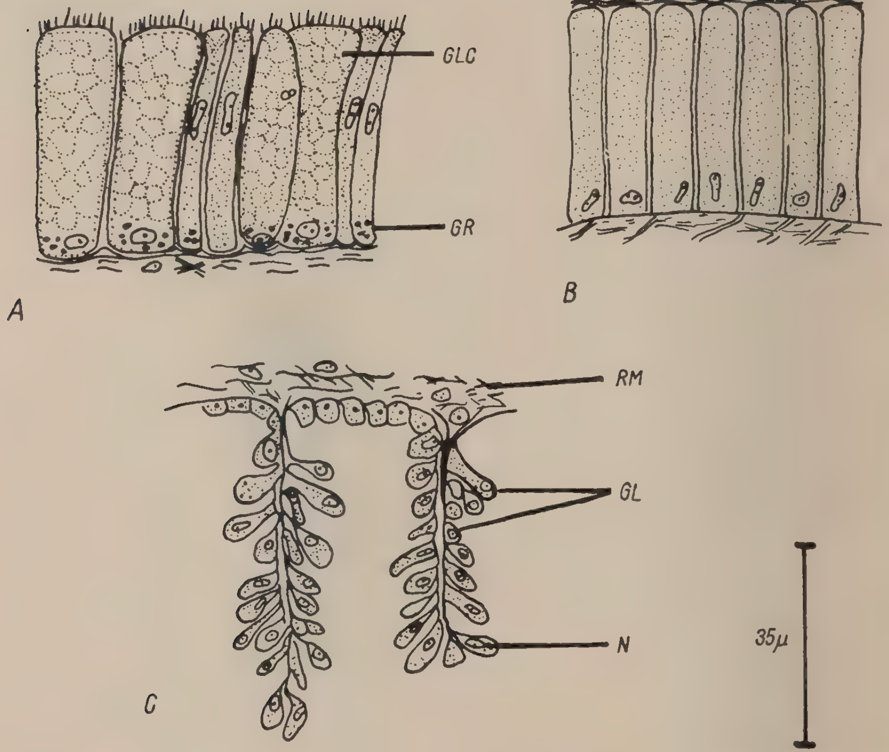

Fig. 3. *Cypraea caputserpentis*. A Epithelium of anterior region of the esophagus (BOUIN's and MALLORY). *GLC* goblet-shaped cells; *GR* granules. B Epithelium of pockets of anterior esophagus (BOUIN's and MALLORY). C Cells of lamellae of mid-esophagus (BOUIN's and MALLORY). *GL* gland cells; *N* nucleus; *RM* radial muscle fibers.

hang over the food channel, the lamellae consisting of clusters of two or three glandular cells (fig. 3C). The cells are attached to a basement membrane which extends through the mid-line of the projections. The wall of the pouch is thin, composed of two or three layers of flat, irregular cells between which muscle fibers are interspersed.

In all examined specimens of *C. caputserpentis* the dilated mid-esophagus is relatively the same size and shape. It is not extensible, and there was no accumulation of food in the pouch of animals collected while feeding. Food is conducted through the mid-esophagus entwined in a mucous string which is confined to the food channel, the only area where ciliary currents were noted. Since the term "crop" or "jabot" implies a structure which accumulates food, and since this region is that portion of the esophagus immediately posterior to the area involved in torsion, the structure is more appropriately termed the mid-esophagus.

The posterior esophagus (fig. 2A, *PE*) is a simple conducting tube opening into the stomach. The histological picture is constant, consisting of tightly packed columnar epithelial cells surrounded by a well-developed layer of circular muscles. There are four prominent folds, two of which are continuations of the food channel, and two of which are formed by variations in thickness of the underlying connective tissue.

The salivary glands form a white lobulated mass lying over the mid-esophagus (*SG*). Although the mass cannot be differentiated into separate glands, two long, narrow, ciliated ducts extend from the mass through the walls of the anterior esophagus and buccal bulb and open into the buccal cavity. The glandular mass is composed of a single type of secretory cell which stains blue with Mallory. The ducts, which are equally well developed, are lined by a simple, ciliated cuboidal epithelium.

c) Stomach and Intestine

The stomach is a U-shaped structure (fig. 4A), the base of which lies ventral to the left border of the visceral mass. The esophagus opens into the left limb anteriorly, and the intestine leaves the right limb near the mid-line of the body. At the internal surface of the base of the U, between the closely attached limbs, an elongate caecum (*C*) forms a ventral projection deeply embedded in the digestive gland. Internally the walls of the left limb or anterior section are longitudinally ridged and grooved (*AS*), the ridges and grooves terminating over a transverse fold (*EF*) on the internal edge of which is an aperture of the digestive gland (*EDA*). The base of the U is a rounded chamber (*CS*) divided by three prominent folds which are oriented to the right toward the caecum (*C*), and between which are fine ridges and grooves which also converge toward the caecum. The right limb is a spacious tube (*CA*) along the floor of which the major typhlosole (*T1*) and the intestinal groove (*IG*) extend, both rising from the caecum. At the intestinal end of the stomach the major typhlosole and intestinal groove are bent sharply to the left, and the small minor typhlosole (*T 2*) appears on the right. Both typhlosoles terminate at the mouth of the intestine, the intestinal groove continuing into the intestine. The walls and roof of the right limb are thrown into a few indefinite folds.

The caecum (fig. 4B, 4C) is a narrow chamber, the floor formed by the major typhlosole (*Tl*) and intestinal groove, the right wall and ceiling by a series of transversely projecting finger-like structures (*CS*) which are continuations of the ridged and grooved area above the caecum, and the left wall consisting of a groove. An aperture of the digestive gland (*CDA*) opens into the lumen at the distal end of the caecum. The groove of the left wall (fig. 4B, *EG*) is histologically distinct from the other portions, the cells staining light yellow with Mallory and containing a granular cytoplasm. The region resembles the efferent groove described by MORTON (1955b) in *Lunella*.

Histologically the stomach proper may be divided into two regions: a ciliated region which is limited to the ridges and grooves of the anterior section and the basal chamber, and a cuticular region which lines the distal section.The ciliated area consists of cells which vary from 80 μ in height in the ridges to 30 μ in the grooves. The cilia are well developed, dense clusters of fibrillae present in the proximal portion of the cells. In the cuticular region the cuticle is thin (2—3 μ) and stains blue with Mallory. It is attached to the distal ends of the cells by a layer of fine projections resembling cilia.

The proximal portion of the intestine is distinguished histologically from the stomach by a region of epithelial cells which bear a prominent ciliary border.

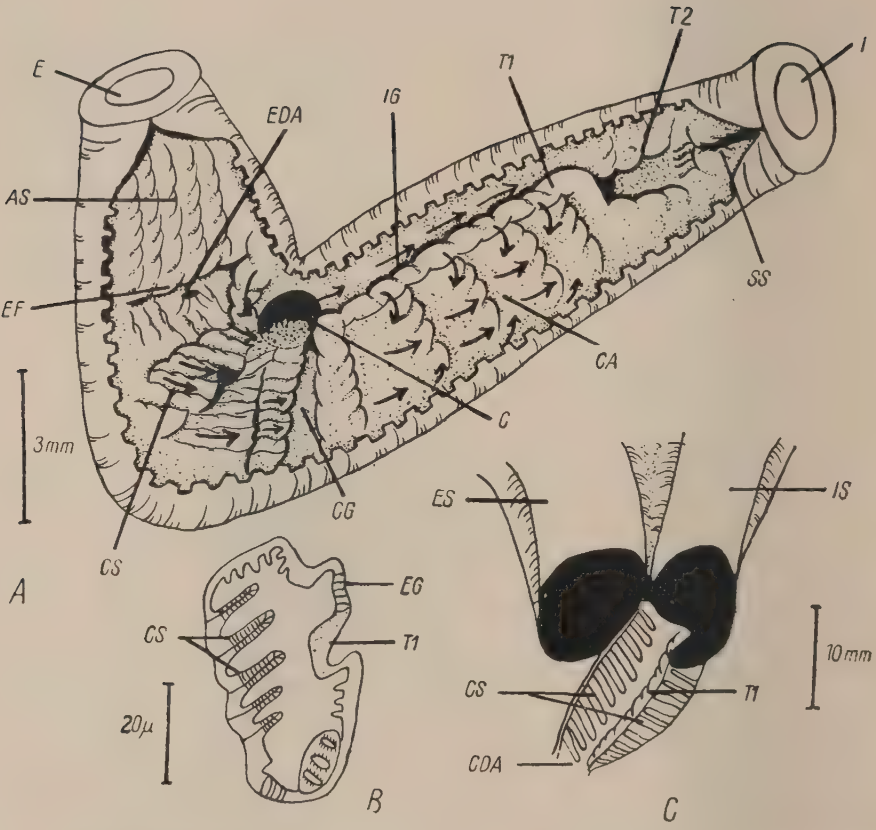

Fig. 4. *Cypraea caputserpentis.* A The stomach opened by a dorsal incision; the esophageal and intestinal ends have been separated. The arrows indicate direction of the ciliary currents. *AS* ridges and grooves of anterior section; *C* caecum; *CA* cuticular area; *CG* channel to caecum; *CS* basal chamber or ciliary sorting area; *E* esophagus; *EDA* aperture of digestive gland; *EF* esophageal fold; *I* intestine; *IG* intestinal groove; *SS* style sac; *T1* major typhlosole; *T2* minor typhlosole. B Diagrammatic section through caecum. *EG* efferent groove; other labels as above. C Diagrammatic view of the relationships of stomach and caecum. *ES* esophageal end of stomach; *IS* intestinal end of stomach; other labels as above.

The lumen of this portion (fig. 4A, *SS*) of the intestine is filled with a compacted faecal mucous rod. Both the distinctive histology and the faecal rod indicate that this region is homologous with the style sac of those molluscs with a crystalline style, the mucous rod or protostyle in *C. caputserpentis* occupying only the proximal portion of the intestine.

Stomach function in *C. caputserpentis* primarily involves the movement of mucous-entangled threads of food material through the caecum and the stomach proper. Material entering the stomach is entangled in a mucous string which spirals out of the esophagus and into the anterior ridged and grooved section of the stomach. Ciliary currents here and in the rounded basal chamber are directed dorsally and posteriorly, except for currents over the area of the anterior section which projecst over the caecum where the currents are directed toward the caecum. As the food string spirals out of the anterior section it divides, a large portion joining the bulky mass of material which fills the chamber of the cuticular section above the intestinal groove and major typhlosole, and a smaller portion moving into the caecum. Topographically and histologically the ridges and grooves of the anterior section and the basal chamber resemble the area described and interpreted as a ciliary sorting area in other prosobranchs. However, a mucus-entangled mass, such as that which emerges from the esophagus of *C. caputserpentis* would not appear to lend itself to a simple mechanical sorting process. Carmine particles introduced into dissected stomachs from which the contents had been removed move in one direction only through the anterior section and basal chamber, toward the distal cuticular region. However, the portion of the ciliated region above the caecum apparently can function as a mechanical sorting device, for when carmine particles are introduced here, the largest particles are immediately rejected and directed into the distal cuticular section. That some sorting does occur is also suggested by the fact that material in the caecum is limited for the most part to particles of microscopical algal origin (although some large particles do occur), and larger particles such as small crustaceans, sponge fragments, and sand grains are confined to the cuticular section.

Within the caecum the mucous food string is passed across the tips of the projections and accumulates near the aperture of the digestive gland, although no particles were actually observed entering the aperture. Two mucous threads are spiralled out of the caecum, one which is carried up the groove of the left wall, joining the material spiralling through the cuticular section of the stomach, and the second (which frequently contains particles resembling those in the absorptive cells of the digestive gland) moving up the intestinal groove to which it is confined during its passage through the stomach. The mucus-entangled mass which moves by clockwise rotation through the cuticular section and the mucous string within the intestinal groove are continuous with the protostyle in the proximal portion of the intestine, and are here consolidated as faecal material. The two strings of waste material are recognizable in both the consolidated faecal mass and the pellets which are finally discharged.

The protostyle in *C. caputserpentis* appears to function only in aiding in the mixing of the stomach contents and in the consolidation of faecal material. While these functions do not include another possible function suggested by MORTON (1952), that of providing the chief source of movement within the stomach by drawing the food-string from the esophagus and sweeping particles across the ciliary sorting area, the apparent functions of the protostyle in *C. caputserpentis* are in agreement with OWEN's (1959) observations on the functions of the protostyle in *Scutus*, and are also compatible with OWEN's (1959) more limited definition of the protostyle as that structure occurring in the proximal portion of the intestine.

The intestine (fig. 4A, *I*) is a uniform tube 50 μ in diameter, extending from the stomach to an anal papilla which lies beneath the mantle on the right side of the body. Except for the proximal portion, the intestine is lined by a sparsely ciliated epithelium which is thrown into folds by variations in the thickness of the underlying connective tissue. A layer of circular muscles similar to that in the posterior esophagus surrounds the intestine. The faecal pellets are ejected through the posterior aperture of the shell.

d) Digestive Gland

The digestive gland is an olive-brown mass which surrounds the stomach and ventral portion of the intestine. It is not obviously divisible into separate lobes. The ducts are lined by a regular columnar epithelium of cell's which may be 20 μ in height, and of which many are ciliated. The cytoplasm of these cells is fairly homogeneous but stains deeply with both Mallory and Heidenhain's iron haematoxylin. Numerous phagocytes occur, intercalated between the epithelial cells, in the lumen, and in the connective tissue surrounding the ducts. The ducts branch into smaller ductules with similar histology and end in the clusters of the digestive lobules.

The lobules of the digestive gland (fig. 5A) are about 100 μ in diameter, and consist of two distinct types of cells corresponding to those which have been described as "digestive" or "absorptive" and "excretory" in other prosobranchs. The "absorptive" cells (*AC*) are the most numerous, 20—30 μ in height, and stain lightly blue or green with Mallory. These cells contain small granules (*G*) which are approximately 3 μ in diameter. Small, darkly staining basal nuclei (*N*) are present. The free surface, which appears to be intact at all times, is convex or irregular in outline. Apparently no cilia are present. Phagocytes (*P*) frequently occur between the absorptive cells and in the lumina of the lobules. The excretory cells (*EC*) are pyramidal in shape and distinguished by yellow or black granules (Mallory) and small nuclei are pressed against the base of the cell. The excretory cells are arranged in crypts which are not always in contact with the lumina of the lobules, but are frequently squeezed between the larger absorptive cells. The

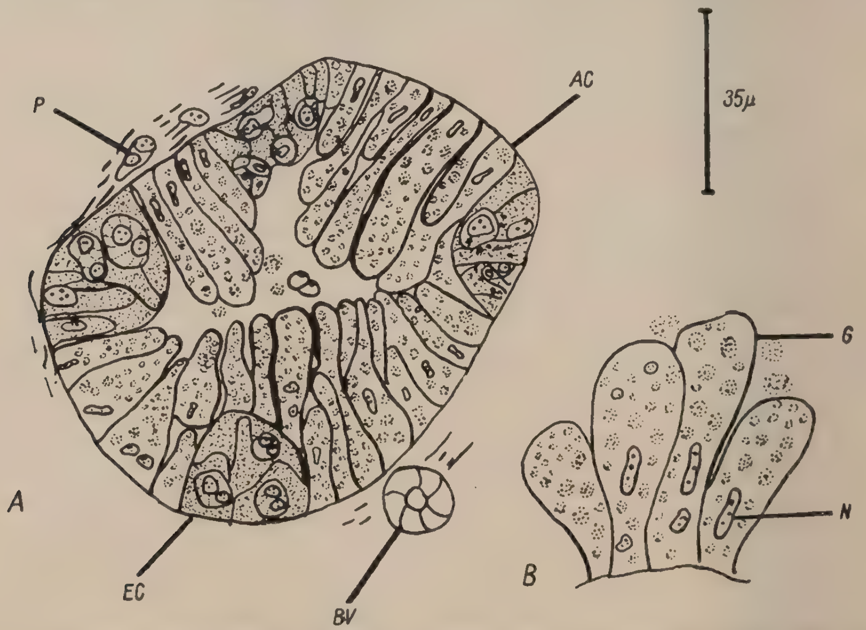

Fig. 5. *Cypraea caputserpentis.* A Lobule of digestive gland. *AC* absorptive cells; *BV* blood vessel; *EC* excretory cells; *P* phagocytes. B Absorptive cells of digestive gland. *G* granules; *N* nucleus. (Fixed in Flemming-without-acetic and stained with eosin.)

granular contents of the excretory cells, however, are present both in the lumina and in the connective tissue between the lobules of the digestive gland.

Digestion in *C. caputserpentis* appears to be largely extracellular. None of the absorptive cells of the digestive gland show any evidence of the ingestion of solid particles. Phagocytosis appears to be limited to wandering cells within the digestive gland. Carbon particles coated with egg white were ingested by phagocytic cells, appearing within the cells surrounded by large vacuoles. Enzymes produced by the digestive gland include an amylase, a protease, and a lipase. Comparison of the amylase and protease with those produced by a known carnivore, *Conus abbreviatus* REEVE (Table 1) shows a strong amylase and a weak protease, which suggest that the food is largely plant material.

Table 1

Enzymes of the digestive glands of *Cypraea* and *Conus*

(1) Amylase: Hydrolysis of 2% Starch Solution

Extracts of digestive gland of a strength of 10% incubated for three hours with 20 cc starch solution, 1% NaCl, 3 cc buffer (6.8).

Titration with sodium thiosulfate (Schoorl's method).

	Cypraea caputserpentis	*Conus abbreviatus*
cc Thiosulfate	7.3	23.0
cc Thiosulfate (control)	28.0	28.0
mg glucose/10 cc	70.0	15.1

(2) Protease: Gelatin Film Substrate

	Cypraea caputserpentis	*Conus abbreviatus*	
Time	12 hrs.	3 hrs.	15 hrs.
pH 2.1	—	+	+
pH 5.6	+	—	+
pH 8.0	—	—	+

(3) Protease: Casein Substrate — Formol Titration

	Cypraea	Control	*Conus*	Control
pH 2.1 . .	—	—	1.1 cc NaOH	—
pH 5.6 . .	1.2 cc NaOH	—	1.6 cc NaOH	—
pH 8.0 . .	0.5 cc NaOH	—	2.0 cc NaOH	—

5. *Reproductive System*

The sexes are separate in *C. caputserpentis*, and it is only by identification of the genitalia that the sex can be determined. Pedal glands are not characteristic of the females as they are in *Trivia* (FRETTER 1946).

a) The Male

Fig. 6A shows the features of the male genitalia. The genital ducts leave the gonad and pass anteriorly and laterally into the region of the pericardium and kidney aperture (*H, KA*). The proximal portion or seminal vesicle (*SV*) is deeply coiled and distended with sperm throughout the year. The epithelium is ciliated

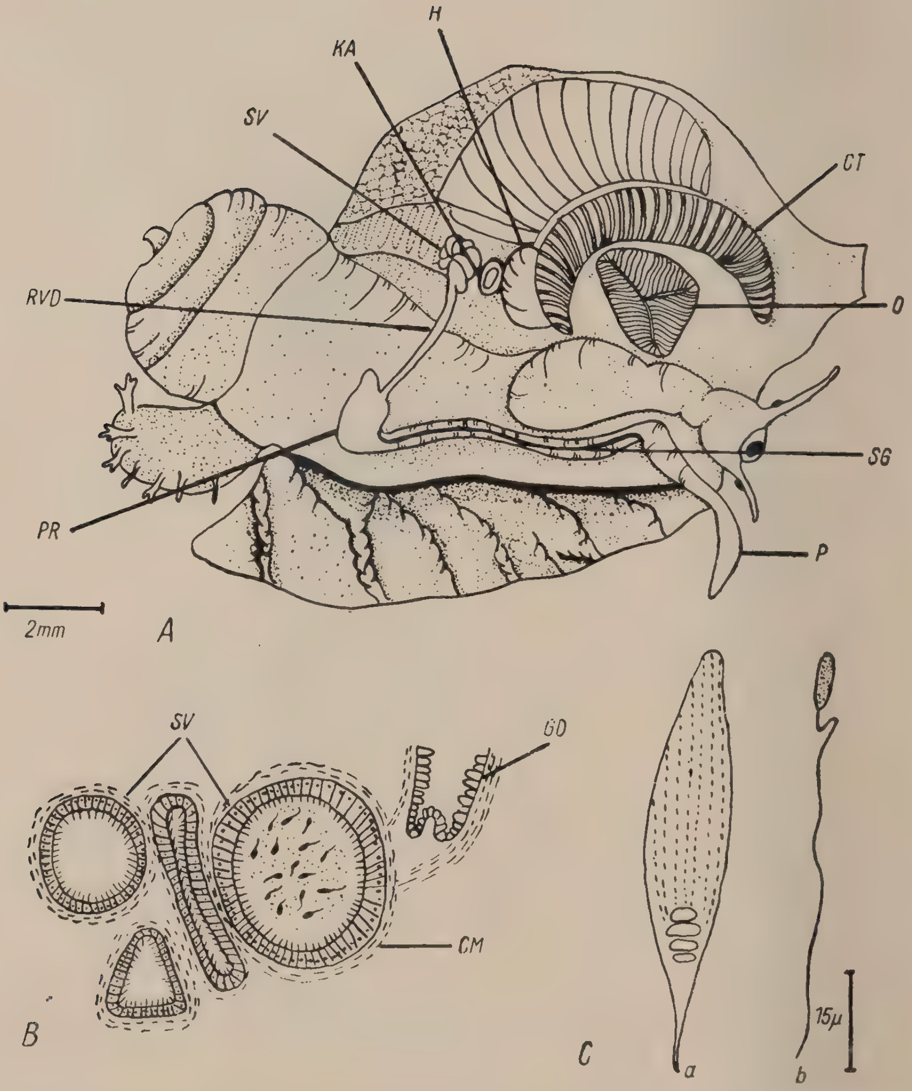

Fig. 6. *Cypraea caputserpentis*. A Male dissected to display the genital ducts. The mantle cavity has been opened from the right side and the mantle and pallial organs turned back. *CT* ctenidium; *H* heart; *KA* kidney aperture; *O* osphradium; *P* penis; *PR* prostate; *RVD* renal vas deferens; *SG* seminal groove; *SV* seminal vesicle. B Transverse section through the coils of the seminal vesicle showing the relationships of the gonopericardial duct. *CM* circular muscles; *GD* gonopericardial duct; *SV* seminal vesicle. C *a* oligopyrene sperm; *b* eupyrene sperm.

and columnar, an irregular basal nucleus with a prominent nucleolus present. A prominent layer of circular muscles is present around the basement membrane of the epithelium. The seminal vesicle merges into the renal vas deferens (*RVD*) characterized by sparsely ciliated cuboidal cells with a vacuolated cytoplasm. Numerous yellow granules are present in the lumen of the vas deferens, around which the sperm are clustered. Near the junction of the seminal vesicle and the renal vas deferens a short strand of tissue extends between the genital duct and the pericardium (fig. 6B, *GD*). Histologically the tissue consists of an outer muscular layer and an inner diverticulum of cells similar to those lining the renal vas deferens. This tissue has been interpreted as the remnant of the gonopericardial duct, similar to that described by LINKE (1933, fide FRETTER, 1941) in *Littorina*. The diverticulum is not in communication with the vas deferens but parallels it for a short distance. Muscular tissue surrounding the diverticulum is similar to that surrounding the vas deferens. The vas deferens enters the thin-walled, bilobed, glandular prostate (fig. 6A, *PR*) postero-laterally. The prostate is completely closed off from the mantle cavity, its walls thickened by a profuse development of gland cells which lie beneath a ciliated epithelium. The gland cells are clumped in oval clusters, the ducts from each cluster running parallel to one another and opening into the lumen between the epithelial cells. The gland cells have rounded basal nuclei which stain lightly with Mallory.

The seminal groove (*SG*) arises from the prostate and forms a deep channel along the right body wall. The edges of the groove are wide enough so that they could form a functionally closed tube. The longitudinal folds of the epithelium are due to differences in height of the columnar ciliated cells of which it is composed. Beneath the basement membrane there is a layer of circular muscles which separate the groove from the body wall. The seminal groove runs up the ventral surface of the penis (*P*), a large tapering structure which is slightly flattened laterally. The penis is a complex muscular structure with dense arrangements of oblique, circular, and longitudinal muscles interspersed with blood spaces.

The testis produces both eupyrene and oligopyrene sperm which have previously been described by BROCK (1887). Both types occur in the lumina of the tubules- The eupyrene sperm (fig. 6C, *b*) possess a short, broad head 3 μ in diameter and a long tail piece. They reach a length of 30—40 μ. The vermiform oligopyrene sperm (fig. 6C, *a*) are 40—60 μ in length, and 10 μ in diameter at their widest portion. These sperm consist of a large cylindrical portion with longitudinal fibrillae and a core of granules in the basal region, and a short tail piece.

b) The Female

The ovary spreads through the visceral mass anteriorly from the tip of the spire, one portion parallel to the posterior esophagus, and the second, larger portion forming most of the third visceral whorl. Fig. 7C shows a dissection of the female genital ducts. The short, thin-walled renal oviduct (*RO*) leaves the gonad near the kidney aperture and runs anteriorly and ventrally on the right side of the visceral mass. It joins the glandular pallial oviduct which extends over the terminal portion of the columellar muscle. The pallial oviduct is comprised of the capsule gland (*RLC*, *LLC*) which receives the renal oviduct, the albumen gland (*AG*) lying at the junction between the renal oviduct and the capsule gland, and the capsule duct (*CD*) which opens into the vagina (*V*). Dorsally a short duct from the albumen gland opens into a diverticulated sac, the seminal receptacle (*SR*), which lies over the albumen gland and the posterior portion of the capsule gland.

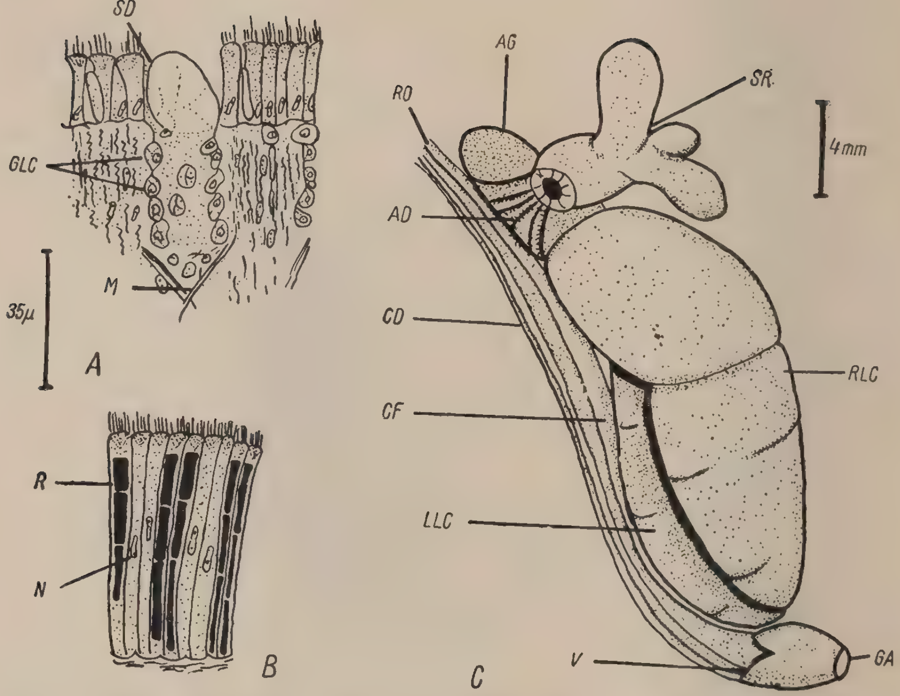

Fig. 7. *Cypraea caputserpentis.* A Cells of the capsule gland (from preparations with BOUIN's fluid and MALLORY). *GLC* gland cells; *M* muscle fibers; *SD* secretion from gland cells. B Cells of albumen gland (from preparations with BOUIN's fluid and MALLORY). *N* nucleus; *R* rods in cells. C Female genitalia from the right; the wall of the albumen gland has been dissected away to show the duct leading into the seminal receptacle, the capsule duct opened, and the lobes of the capsule gland separated. *AD* duct leading to seminal receptacle; *AG* albumen gland; *CD* capsule duct; *CF* fold; *GA* genital aperture; *LLC* left lobe of capsule gland; *RLC* right lobe of capsule gland; *RO* renal oviduct; *SR* seminal receptacle; *V* vagina.

The ovarian duct is ciliated, the epithelium resembling that of the ovary itself. The cells stain green with Mallory. The glandular lining of the ovarian duct is replaced by a ciliated columnar epithelium in the renal oviduct, variations in thickness of the underlying connective tissue resulting in several folds along the walls. The duct is surrounded by a coat of longitudinal and circular muscles. A vestige of the gonopericardial duct with an epithelium similar to that of the renal oviduct is present, terminating as the oviduct enters the capsule gland.

The albumen gland is an elongate bilobed structure with a ciliated columnar epithelium lining the lumen. The walls are thickened by subepithelial gland cells which are filled with regularly shaped rods (fig. 7B, *R*) staining deeply with Heidenhain's iron haematoxylin and Mallory. Within the lumen both eupyrene and oligopyrene sperm are present, embedded without orientation in a thick mucous string. The epithelium of both the duct leading from the albumen gland into the seminal receptacle and the receptacle is ciliated. Within the seminal receptacle the sperm are oriented with the heads buried in the distal cytoplasm of the epithelial cells, the tails projecting toward the lumen.

The capsule gland is an opaque white or yellow mass divided into right and left lobes which attain a thickness of 1.5—2 mm. The lobes are composed of several distinct glandular areas indicated macroscopically by color differences and histologically by differences in cell structure and staining properties. Gland cells arranged in clusters running parallel to one another and opening between the ciliated epithelial cells into the lumen form the major portion of the gland (fig. 7A). The cells are interspersed with muscle fibers (*M*) and connective tissue. The gland cells (*GLC*) are small (6 μ), roughly cuboidal, and stain lightly with both Mallory and Heidenhain's iron haematoxylin. A layer of more deeply staining gland cells at the lateral edge of the right lobe of the gland makes this lobe thicker than the left. In the ventral portion of the left lobe the gland cells are larger than those of the other portions, and stain light blue with Mallory. The lumen is lined by a regular ciliated epithelium. Ciliary currents are in the direction of the genital aperture.

The lobes of the capsule gland are joined anteriorly by a thin suture and posteriorly by a wall continuous with the capsule duct but separate from it by a narrow fold (fig. 7C, *CF*). This fold divides the oviduct into a narrow channel adjacent to the capsule gland and a wider channel laterally. Both fold and duct are lined by a ciliated columnar epithelium, the cilia of which beat toward the albumen gland and seminal receptacle. The capsule duct leads into a vestibule which is lined by a deeply staining epithelium and which is surrounded by a thick layer of circular muscles. The vagina proper is anterior to the vestibule, distinguished by deeply folded walls.

Although copulation was not observed, it is inferred from the structure of the genitalia that the penis is inserted into the genital aperture and extends at least some distance into the capsule duct. Accomodation of the penis in the capsule duct may be accomplished by compression of the lumen of the capsule gland, the muscles present in the gland permitting compression and expansion of the structure. The fold which partially divides the capsule duct from the gland would function in closing off the gland as the penis is inserted. More sperm are ejected during copulation than are utilized in fertilization of eggs deposited at one time, and these sperm are accumulated in the seminal receptacle. Sperm remain active in the receptacle for at least eleven days following copulation.

6. *Egg Deposition and Development*

Observations on the mode of deposition of the egg capsules were made possible when one specimen deposited eggs on the glass wall of a salt water aquarium. Approximately 48 hours before the appearance of the egg capsules, the female took up a position on the wall of the aquarium. During the entire period of egg deposition the shell was covered by the mantle. While remaining in the area circumscribed by her foot, the animal constantly circled over the substrate, displaying continuous radular activity against the glass wall. During this period of activity the usual oval shape of the foot gradually changed to a quadrangular shape, and the posterior portion divided so that a shallow groove (fig. 8A, *GR*) channeled the surface of the foot, ending in the mid-region of the sole as a deep pore (*P*). The anterior groove (*AG*) of the foot was more conspicuous than usual, this feature perhaps due to the pressure of the foot against the substrate. The left side of the foot was distinguishable from the right by a series of small white

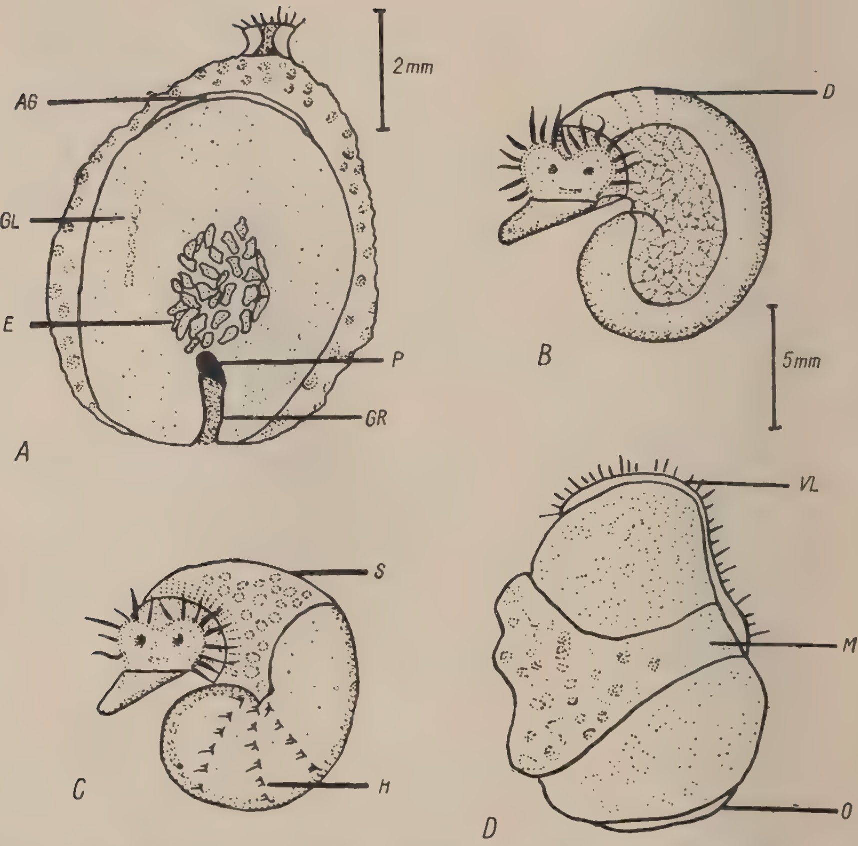

Fig. 8. *Cypraea caputserpentis.* A Female depositing egg capsules. *AG* anterior channel; *E* egg capsules; *GL* glandular structures; *GR* groove; *P* pore. B Veliger showing development of dots on first whorl. *D* dots. C Veliger showing development of shield and hair-like projections. *H* projections; *S* shield. D Metamorphosing larva with mantle, veliger lobes, and operculum. *M* mantle; *O* operculum; *VL* veliger lobes.

structures (*GL*) which were visible through the transparent epithelium. These structures were not obviously in communication with the exterior, nor was any secretion noted. The egg capsules were emitted from the posterior aperture of the shell, and by muscular contractions of the foot moved along the groove toward the mid-region of the foot where they were attached to the substrate. Approximately 200 egg capsules were deposited in a period of six hours. Once deposition of the egg capsules had ceased, the female continued to circle over the egg mass, and eventually rasped all of the capsules from the substrate so that further observations on development were not possible. Within seconds after the last capsule had been rasped from the substrate, the foot resumed its normal shape and the animal moved away from the site of deposition. Under natural conditions the females of *Cypraea* are known to "brood" over their egg capsules for periods of two weeks (OSTERGAARD 1950, NATARAJAN 1954).

There is apparently no specific breeding season for *C. caputserpentis* in Hawaii. Egg masses have been collected during various months of the year; the gonads appear to be about the same size and color when examined periodically; and sperm have been removed from the seminal receptacles of adult females examined monthly over a period of two years.

Egg masses measuring 2—3 cm in length and 1—2 cm in width are attached to the undersurfaces of rocks and coral. The masses conform to the contours of the substrate, but in general outline resemble the foot of the animal and are somewhat flattened. Between 100—200 transparent capsules are in each egg mass, adhering three and four deep in a gelatinous matrix, the long axis of the case horizontal. The capsules are of varying shape, some oblong, others constricted and vase-shaped. The capsules measure about 1.1 mm in length and 0.9 mm in breadth and contain approximately 200 eggs.

Newly deposited eggs are white and measure about 90 μ in diameter. The incubation period appears to be about 18 days, trochophoral stages appearing three days after collection of uncleaved eggs, the veliger stage 12 days later, and the veligers hatching out after another three days. Several instances of the occurrence of both trocophoral stages and veliger stages in the capsules of a single egg mass were recorded. This indicates that the egg capsules are not deposited simultaneously, a suggestion which is compatible with the observation noted above of the occurrence of active sperm in the seminal receptacle for periods of at least 11 days after copulation.

The newly hatched veligers measure 1—1.2 mm across the widest portion of the shell. The velum is bilobed and measures 0.9 mm across the lobes. The shells are light yellow in color and pitted with shallow depressions. The operculum is the same color as the shell, and there is a reticulated pattern on the external surface.

Approximately two hours after escaping from the egg cases the veligers increase the speed of their swimming movements, a period of vigorous activity ensuing for about 15 minutes. The larvae then come to rest on the substrate. During the activity period a series of dots radiating from the center of the shell develops (fig. 8B) and after the larvae have ceased their vigorous movements the dots on the first shell whorl enlarge and become lumpy in appearance. The lumps gradually coalesce, forming a shield about 84 μ in diameter. Simultaneously the dots on the lower portion of the shell gradually increase in size and develop hair-like projections (fig. 8C). The development of the shield and projections occupies about one hour. The animals remain relatively inactive for the next 12 hours, at the end of which time they have elongated, and the shield has developed three knob-like projections (fig. 8D). The velar lobes are still present, protruding from the ventral surface anteriorly and the operculum extends posteriorly. Further observations on metamorphosis have not been possible up to the present.

III. AN INTERPRETATION OF RELATIONSHIPS AMONG THE CYPRAEACEA

The picture of *C. caputserpentis* which emerges from the above descriptions, and which appears to be characteristic of the other species of *Cypraea* (KAY, mss in press), is that of a browsing gastropod with many of the features of the idealized primitive prosobranch as it has been interpreted by Graham (1939) and Morton (1955a). Although the Cypraeacea are in general recognized as highly organized prosobranchs, *Cypraea* appears to have retained many of the ecological and anatomical features attributed to the ancestral prosobranch stock, while the other genera included in the Cypraeacea are more specialized in habitat and modified in anatomy.

The species of *Cypraea* are in general associated with the occurrence of coral reefs where they occupy a wide variety of habitats within their distributional range. Both the shell and mantle of *Cypraea* are noted for their brilliant coloring, however no generalization can be drawn at present regarding a correlation between either mantle or shell color and the habitats of the animals. Where data are available for other cypraeid genera, it appears that these genera are considerably restricted in habitat. *Trivia*, *Erato*, and *Simnia* are associated with sessile ascidians in British waters (Lebour 1932, 1933a, 1933b; Fretter 1951), and the author has observed *Trivia* on ascidians in the waters of the Hawaiian Islands. In the Pacific *Ovula ovum* (L.) occurs on alcyonarians (Demond 1957); and along the coasts of the Americas *Primovula*, *Neosimnia*, and *Pedicularia* are associated with gorgonids (Abbott 1954). The shell and mantle of these genera tend to approximate the background color and texture of the habitat. In *Trivia* animals with white mantles and shells occur on white ascidians in the Hawaiian Islands (Kay, unpublished observation). *Neosimnia* of the Atlantic coast of North America is a deep lavender on the purple sea fan *Leptogorgia hebes* Verrill and yellow on the yellow sea fan *Leptogorgia virgulata* Lam.; and *Pedicularia californica* Newcomb of the California coast is red, simulating the color of the hydrozoan *Allopora californica* Verrill with which it is associated (Abbott 1954). The shells of *Neosimnia* and other Amphiperasiinae which occur on the branches of gorgonids are longer and narrower than in either *Cypraea* or *Trivia*, and the shell of *Pedicularia* is flattened and closely attached to the coralline substrate on which it occurs. In *Cypraea*, which crawls freely over a coral or sand substrate, the foot is without distinctive glandular equipment. The glandular equipment of *Trivia*, *Erato*, and *Simnia* which consists of a posterior mucous gland in addition to the anterior pedal gland appears to be characteristic of many small molluscs (Fretter 1947, 1951).

The taenioglossan radulae of all cypraeid genera display differences in tooth structure which can be associated with different diets. The radula of *Cypraea* is reminiscent of the radula of archaeogastropods such as *Lunella* (Morton 1955b) in function if not in structure, all of the teeth serving in scraping particulate matter from the substrate. In *Trivia*, *Erato*, and *Simnia*, which feed on sessile ascidians (Lebour 1932, 1933a, 1933b; Fretter 1951), and in *Ovula ovum* and *Pedicularia* (the food habits of which are not known) the teeth are distinctly serrated and the laterals well-developed. In *Simnia* and *Ovula* the laterals are rhipidoglossan in appearance, consisting of numerous basally fused uncini which in *Simnia* brush up tissues loosened by other radular teeth (Fretter 1951). Jaws are present in addition to the radula in *Trivia*, *Simnia*, and *Erato* (Vayssière 1923, Fretter 1951), furnishing additional cutting surfaces.

The alimentary canal of the Cypraeacea shows few of the modifications of structure characteristic of carnivorous gastropods. There appears to be a general tendency, however, toward the development of a glandular area in the region of the anterior esophagus. In *Cypraea* the region is distinguished only by a pair of histologically distinct pockets; in *Trivia* the ventral wall is formed by mucous cells (FRETTER 1951); and in *Erato* the mucous wall is separated off as a ventral, glandular diverticulum (FRETTER 1951). The mid-esophagus is characterized by lateral pouches with deeply folded walls in *Trivia*, *Erato*, and *Simnia* (FRETTER 1951), similar to the pouches which are considered characteristic of the primitive condition. The single, large glandular pouch in *Cypraea* may perhaps be explained in terms of an expansion and fusion of the primitively occurring series of small pouches. The posterior esophagus in all genera is a simple conducting tube.

The stomach of *Cypraea* agrees in many respects with those features suggested by GRAHAM (1939) with MORTON's (1953) modifications as characteristic of the ancestral prosobranch stomach. These features include its division into a proximal globular region with a ciliary sorting area converging on the intestinal groove, a distal tubular style sac which MORTON (1953) has suggested in the primitive condition contains a compacted faecal rod or protostyle, and a caecum into which the major typhlosole extends. The stomach of *Cypraea* differs from the primitive condition in that the proximal region is a straight tube, only a small portion retaining a suggestion of the globular shape, and the ciliary sorting area while structurally present does not function as a mechanical sorting device. A caecum is present only in *Ovula* (KAY, unpublished observation) of the other cypraeid genera of which the anatomy is known. In *Trivia*, *Simnia*, and *Erato* the stomach is clearly similar to that in *Cypraea* but is in general simpler. It is generally recognized that the stomach is less complex in those animals with a carnivorous habit. The stomach of *Trivia* differs from that of *Cypraea* in that it lacks a caecum, and a small gastric shield is present in the ciliary sorting area (GRAHAM 1939).

There is considerable evidence that the genital ducts of the mesogastropods were open in the ancestral stock (FRETTER 1952). The seminal groove in *Cypraea*, *Ovula* (KAY, unpublished observation), and the partially open duct of *Simnia* (FRETTER 1951) may thus be accounted for in terms of the presumably primitive condition, while the closed ducts of *Trivia* and *Erato* (FRETTER 1951) are indicative of a more specialized system. In *Cypraea* and *Simnia* the prostate does not open into the mantle cavity, whereas in *Trivia* and *Erato* the prostate communicates with the mantle cavity (FRETTER 1946, 1951). FRETTER (1946) has suggested that the opening of the prostate into the mantle cavity in forms having a seminal duct may result in selection advantages in that excess seminal fluid can escape and the possibility of rupture of the genital ducts is reduced. In all genera the penis is a large, non-invaginable structure. The genital aperture of the females of *Cypraea* and *Simnia* (FRETTER 1951) is terminal. In some species of *Cypraea* a bursa copulatrix is present, lateral to the genital aperture, and in these species the seminal receptacle is glandular rather than saccate (KAY, mss in press), and macroscopically similar to those described by FRETTER (1946) in the stenoglossans *Nucella* and *Ocinebra*. In the females of *Trivia* and *Erato* the capsule gland opens laterally into the mantle cavity (FRETTER 1946, 1951). Although females of *Trivia* may be distinguished from males by the occurrence of a pore in the mid-ventral surface of the foot into which the ventral pedal gland opens (FRETTER 1946), there is no such permanent pore in the foot of *Cypraea*, a transient groove and pore appearing during the deposition of egg capsules. *Cypraea* deposits eggs on any hard substrate while the eggs of *Simnia*, *Trivia*, and *Erato* are deposited on or in compound ascidians (LEBOUR 1932, 1933a, 1933b; FRETTER 1951). The larval stage is a simple veliger in *Cypraea* and *Simnia* (LEBOUR 1932); an echinospira is present in *Trivia* and *Erato* (LEBOUR 1933a, 1935).

Although the nervous system has not been described in this work, it should be noted that in all cypraeid genera the cerebro-pleural ganglia are concentrated such that there is little or no indication of a cerebro-pleural connective, and in *Trivia* and *Erato* the pedal ganglia are also concentrated near the cerebro-pleural mass. The pedal nerve cords of *Cypraea*, *Ovula*, and *Simnia* are diffuse, extending the length of the foot. Both Thiele (1931) and Schilder (1936) regard the long pedal nerve cords as secondarily derived; however, the occurrence of primitive features in the digestive and reproductive systems of these genera suggests that the long pedal nerve cords are also primary archaic characters.

The available data on the biology and anatomy of the genera included in the Cypraeacea indicate that the general tendency within the group is toward a carnivorous, sessile habit, and the various features of the cypraeid plan as they appear in the browsing form *Cypraea* are correspondingly modified. In those genera which are restricted in habitat both mantle and shell tend to approximate the background color and structure of the habitat; the teeth of the taenioglossan radula are serrate and specialized, and jaws are present, both which are modifications associated with a carnivorous diet; and the stomach is simplified, particularly by the loss of the caecum characteristic of microphagous gastropods. The primitive position of *Cypraea* is further indicated by the occurrence in the other cypraeid genera of specialized features which are not directly associated with a restricted habitat and diet: the reproductive system with closed genital ducts in the males and the nervous system with concentrated pedal ganglia.

The Cypraeacea may perhaps best be characterized as a group of molluscs in which the features diagnostic of each genus are to be largely associated with specialized habitats and diets. Within the Cypraeacea the Cypraeinae (*Cypraea*), Amphiperasiinae (*Simnia*, *Ovula*, *Neosimnia*, *Volva*), and Pediculariinae (*Pedicularia*) possess common features as regards the digestive, reproductive, and nervous systems, but both the Amphiperasiinae and Pediculariinae are specialized in habitat and diet and correspondingly modified in shell and radular characters. The Triviinae (*Trivia* and *Erato*) with closed reproductive ducts and concentrated pedal ganglia, as well as with anatomical modifications associated with restricted habitats and diets, have diverged even further than have the Amphiperasiinae and Pediculariinae from *Cypraea*.

The author wishes to thank Dr. A. J. Kohn for providing material for study of the early developmental stages. For reading and criticizing the manuscript and for much valuable discussion, the author is indebted to Dr. R. W. Hiatt and Dr. A. J. Bernatowicz. This paper is Contribution No. 130 from the Hawaii Marine Laboratory.

IV. SUMMARY

The gastropod *Cypraea caputserpentis*, studied in the Hawaiian Islands, is a generalized browsing form with many of the features of the idealized primitive prosobranch. The radula is of typical taenioglossan arrangement, all of the teeth serving as raking or scraping tools. The alimentary canal deals with small particles principally of algal origin, and there is an emphasis on ciliary action and mucus production in the esophagus and stomach. The mid-esophagus is dilated, the surface increased by lamellae which project over the dorsal food channel. The stomach is characterized by an antero-ventrally directed caecum and a short style-sac region at the proximal end of the intestine. Faecal pellets are compacted in the intestine. The reproductive system of the male is distinguished by an open

seminal groove, and the prostate is closed off from the mantle cavity. In the female the genital aperture is terminal. The seminal receptacle is a diverticulated sac lying dorsally between the capsule and albumen glands. Eggs are deposited in capsules which are attached to a hard substrate. The female "broods" the egg mass. The larval stage is a free-swimming veliger, and development up to metamorphosis is estimated at about 18 days.

Comparison of the biology and anatomy of *Cypraea* with other cypraeid genera suggests that within the Cypraeacea *Cypraea* has retained many of the features of the ancestral prosobranch stock, while other genera such as *Trivia*, *Erato*, *Simnia*, etc. are restricted in habitat and modified in anatomy.

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Reprinted from PACIFIC SCIENCE, *vol. XIV, no. 3, July, 1960*

Two New Species of *Candacia* (Copepoda: Calanoida) from the Central Pacific, with Notes on Two Other Species[1]

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DURING EXAMINATION of plankton samples collected from the central Pacific Ocean by the Honolulu Biological Laboratory (formerly Pacific Oceanic Fishery Investigations) of the U. S. Fish and Wildlife Service, two species of *Candacia* were found which appear to be undescribed. In addition to describing these two species we present evidence that *Candacia turgida* Wilson is a synonym of *C. truncata* (Dana). We also include a description and figures of *Candacia norvegica* (Boeck), a species apparently rare in the Pacific Ocean.

We wish to acknowledge the help of Dr. Thomas E. Bowman in loaning us type material from the U. S. National Museum, and that of Dr. Paul L. Illg for valuable suggestions during the preparation of the type material and the manuscript.

Candacia pofi new species
Figs. 1–21

LOCALITY AND MATERIALS: 1° 23′ S., 112° 46′ W. (U. S. Fish and Wildlife Service "Hugh M. Smith" cruise 31, station 75-3, Oct. 31, 1955, 200–140 m. depth of tow; 23 females and 6 males). Physical, oceanographic, and other data from this cruise have been published by King, Austin, and Doty (1957).

Type material of *Candacia pofi* has been deposited in the U. S. National Museum as follows: Female holotype (USNM 102730), male allotype (USNM 102731), 22 female paratypes and 5 male paratypes (USNM 102732).

MEASUREMENTS: Measurements were made from a dorsal view along a sagittal plane. The abdomen was supported by a plastic strip to reduce flexion. The copepod, stained with methyl blue and immersed in lactic acid, was mounted under a cover slip supported by plastic strips to avoid distortion due to pressure or a meniscus. The total length was measured from the anterior margin of the head to the ends of the caudal furca. The abdomen was measured from the anterior margin of the genital segment to the ends of the caudal furca. These measurements excluded the telescoped portions of the abdominal segments. The ratios of the lengths of the abdominal segments, however, include the telescoped portions as indicated by dotted lines in the figures. Pertinent measurements and ratios of the cephalothorax and abdomen of the holotype, allotype, 3 female paratypes, and 4 male paratypes are given in Table 1.

DESCRIPTION: In the adult female the cephalothorax (Fig. 1) is slender, being widest at the first thoracic segment. The posterior lateral angles of the thorax are produced into sharp symmetrical processes which reach to a line including 60 per cent of the length of the genital segment (Fig. 3). The genital segment (Fig. 3) is symmetrical in dorsal view, longer than wide and without lateral swellings or processes. The genital pore is situated on a very large protuberance which extends ventrad and caudad. In lateral view (Figs. 2, 4), the posterior margin of this protuberance is approximately continuous with the posterior margin of the genital segment. In ventral view (Fig. 5), the genital protuberance is round with a slight lip at the posterior margin. In the holotype, this lip is slightly asymmetrical. The second abdominal segment (Fig. 3) is asymmetrical in dorsal view, the right margin being convex and the left margin straight. The ventral surface is wrinkled and bears a low process which extends to the left as a lobe with a more or less crenulate margin.

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[1] Contribution No. 131, Hawaii Marine Laboratory, University of Hawaii, with which one of the authors (G. D. G.) was associated. Manuscript received January 16, 1959.

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The dorsal surface of the anal segment (Fig. 3) bears a very prominent, broad bifurcate process pointing caudad. The posterior lateral surface of each of the diverging tubercles of this process has a patch of very fine teeth visible under 100× magnification. In the holotype, these tubercles appear to be slightly asymmetrical in size and in details of minute swellings and creases. Examination of paratype material indicates that there is variation in these details and also in the ventral lobe of the second abdominal segment.

The furcal rami (Fig. 3) are longer than wide. The outermost furcal setae are thick and originate high on the lateral margins of the rami. There is a small tooth dorsad of the origin of the middle major seta of each ramus.

The proximal seven segments of the first antennae are thickened. The first segment has three small spines, and segments 2 through 6 have small marginal spines (Fig. 6). It is probable that additional segments had spines which have been lost in the material at hand.

The second antennae are similar to those of other members of the genus. The exopod has six setae plus a minute one; the second endopodal segment is divided into two lobes, the external with six setae plus a minute one and the internal with five setae plus a minute one.

The exopod of the mandibular palpus has five setae; the endopod has six. The mandibular blades (Fig. 7) are composed of a large point and a basal tooth with three points decreasing in length mediad.

The first maxillae are best described by reference to Figure 8.

The second maxillae (Fig. 9) are large and have the form of maxillipeds. The basal segment is composed of four lobes. There is a single long seta on the first lobe with a minute seta at its base, two small setae on the internal margin of the second lobe, and one large spine with a short spine at its base on each of the third and fourth lobes. There are two long spines of about equal length on the second basipodal segment, and the proximal one has a minute spine at its base. Distad of the second basipodal segment are three very long, curved spines, the middle of which is the longest. Three very small bristles arise from the base of the distal spine.

The maxillipeds are reduced in length (Fig. 10). The first segment is about as long as the remaining segments combined and is 1.7 times the length of the second. There is a tubercle on the internal margin of the first segment near the proximal end and a single long seta just distad of the midpoint of that margin. Two slender setae, one twice the length of the other, arise from the junction of the first and second segments. At about the midpoint of the internal margin of the second segment, there is a patch of hair proximad of three setae. The distal end of this segment appears to receive the proximal end of the third so that the second and third each have three setae. Vervoort (1957), in describing *C. maxima,* attributes four setae to the second segment and two to the third. Giesbrecht (1892, pl. 21, figs. 26, 27) indicates that in *C. longimana* Claus the fourth seta is between the two segments but in *C. bispinosa* Claus it is on the third segment. This appendage is usually regarded as having little diagnostic value, but the origin of the fourth seta might add a distinguishing character. The fourth, fifth, and sixth segments have a pair of setae, the distal one in each pair being longer. Distad of the sixth segment are two long setae of almost equal length.

The lengths of the third exopodal segments of swimming feet 1 to 4 (Figs. 11–14) have the following relation to that of their respective terminal spines: 1:1, 2:1, 3:1, and 3:2.

The symmetrical fifth feet (Fig. 15) are long and slender, each ending in two sharp, smooth terminal fingers. The inner finger is about four times the length of the outer finger. There are two external spinous processes located at points about one-fourth and two-thirds of the segment length from the proximal end of the distal segment. There are no internal spines or setae. The penultimate segment bears a single seta, and the ratio of the length of that segment to that of the distal segment is 1:4.6.

Brown pigmentation in the female is restricted to the following structures: the fifteenth segment of the first antennae, the setae of the second antennae and the mandibular palpi, the second segment of the second max-

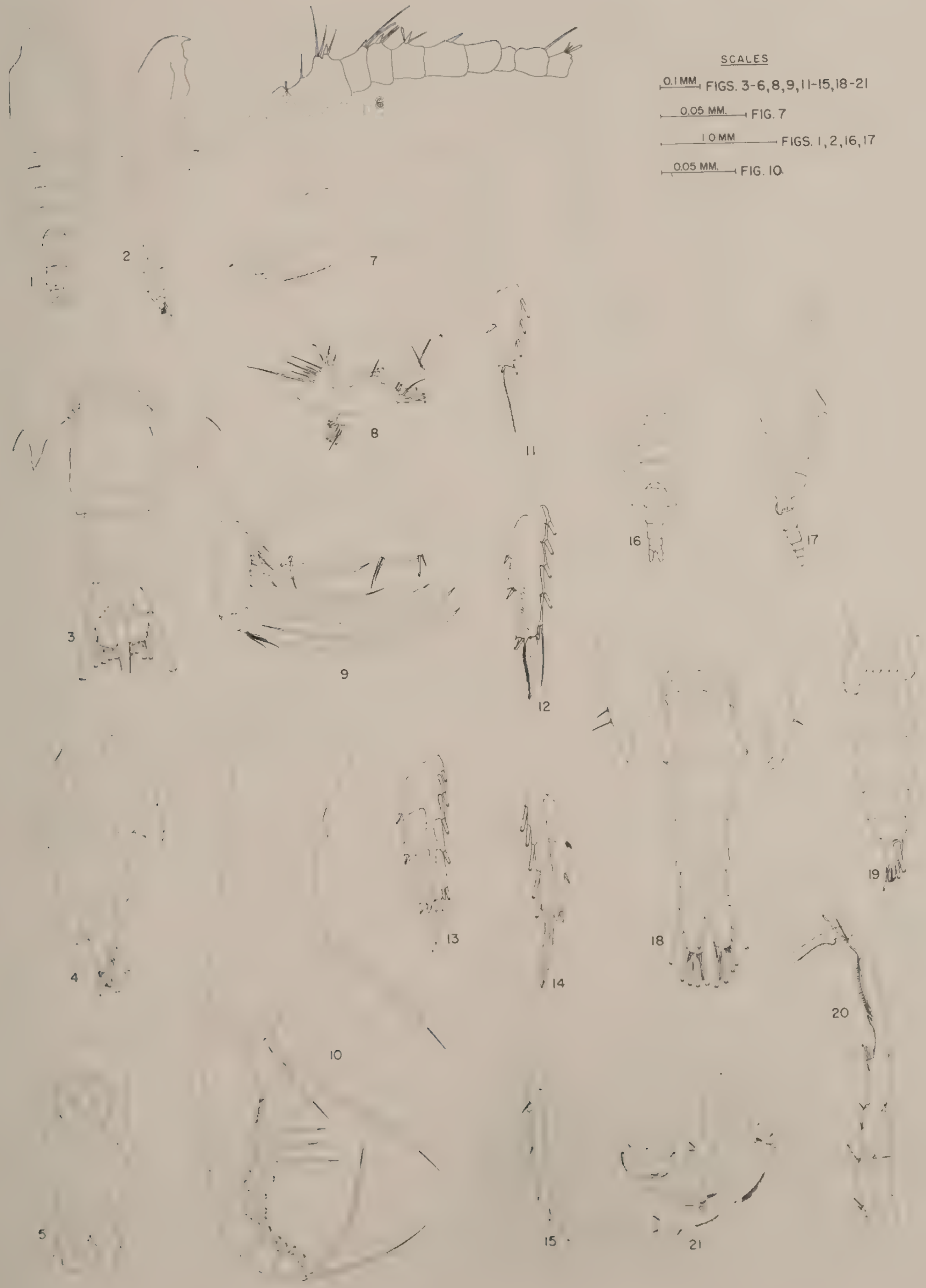

SCALES
0.1 MM. FIGS. 3-6, 8, 9, 11-15, 18-21
0.05 MM. FIG. 7
1.0 MM FIGS. 1, 2, 16, 17
0.05 MM. FIG. 10

TABLE 1
TOTAL LENGTHS, CEPHALOTHORAX–ABDOMEN RATIOS, AND ABDOMINAL SEGMENT RATIOS OF *Candacia pofi*

SPECIMENS	TOTAL LENGTH (mm.)	CEPHALOTHORAX–ABDOMEN RATIO	RELATIVE LENGTH OF ABDOMINAL SEGMENTS					
			1	2	3	4	5	Furca
Females								
Holotype	2.30	2.75:1	38	32	16	...	...	14 = 100
Paratype	2.41	2.64:1	42	30	16	...	...	12 = 100
Paratype	2.41	2.55:1	41	32	16	...	...	11 = 100
Paratype	2.36	2.75:1	39	29	17	...	...	15 = 100
Males								
Allotype	2.28	2.52:1	21	21	21	14	9	14 = 100
Paratype	2.21	2.61:1	21	21	21	14	9	14 = 100
Paratype	2.24	2.38:1	21	21	21	14	9	14 = 100
Paratype	2.23	2.54:1	...	...	...	...	...	... ...
Paratype	2.21	2.43:1	...	...	...	...	...	... ...

illae, the third exopodal segments of swimming feet 1 to 4, and the furcal setae.

The pertinent measurements and ratios of the adult males are presented in Table 1. The posterior lateral angles of the male cephalothorax (Fig. 16) are produced into asymmetrical processes. The left is sharp and reaches to the posterior margin of the genital segment. The right process (Fig. 18) is thick and slightly curved inward and reaches to a line including one-quarter of the length of the second abdominal segment. In lateral view (Figs. 17, 19), this right process is thick and truncate with a convex dorsal margin and a concave ventral margin.

The male genital segment (Fig. 18) is asymmetrical with a rounded swelling tipped with a small button on the right side. In lateral view (Fig. 19) the swelling appears as two or three concentric, incomplete circles. The left posterior margin of the genital segment is broken by the genital opening. In the allotype, a canal is visible from the genital opening to a spermatophore (Fig. 18).

The geniculate right antenna (Fig. 20) is armed with coarse, unequal pigmented teeth on segment 18, fine pectination on segment 17 extending onto the anterior margin of a distal spinous process, and very fine pectination on segment 19. Segments 17, 18, 19, and 20 are separate.

The right fifth foot (Fig. 21) is chelate with the tip of the distal segment reaching slightly beyond that of the penultimate segment. The terminal spine is turned flat against the surface of the distal segment. The left fifth foot is broad and ends in a spatulate segment (Fig. 21).

Pigmentation is similar to that of the female. In addition, the geniculate portions of the right first antenna are heavily pigmented. There is no pigmentation on the right thoracic process or the genital segment.

REMARKS: The female of *C. pofi* resembles *C. cheirura* Cleve (as described by Farran, 1929) in having ventral protuberances on the genital and second abdominal segments, and thick ex-

FIGS. 1–21. *Candacia pofi* n. sp. 1, female, dorsal view; 2, female, lateral view; 3, fourth and fifth thoracic segments and abdomen, dorsal view, female; 4, fourth and fifth thoracic segments and abdomen, lateral view, female; 5, abdomen, ventral view, female; 6, proximal 10 segments of first antenna, female; 7, mandibular blade, female; 8, first maxilla, female; 9, second maxilla, female; 10, maxilliped, female; 11, third exopodal segment of first foot, female; 12, third exopodal segment of second foot, female; 13, third exopodal segment of third foot, female; 14, third exopodal segment of fourth foot, female; 15, fifth foot, female; 16, male, dorsal view; 17, male, lateral view; 18, fourth and fifth thoracic segments and abdomen, dorsal view, male; 19, fourth and fifth thoracic segments and abdomen, lateral view, male; 20, segments 13 through 19, right first antenna, male; 21, fifth feet, male. Figures 1–12 and 15 drawn from holotype; Figures 13 and 14 from paratype. Figures 16–19 and 21 drawn from allotype; Figure 20 from paratype.

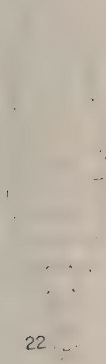
SCALES

0.5 MM FIGS. 22, 23, 36, 37

0.05 MM FIGS. 27, 30, 35

0.1 MM. FIGS. 28, 31-34, 40, 41

0.1 MM. FIGS. 24-26, 29, 38, 39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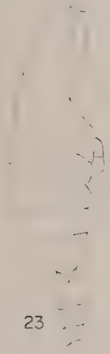
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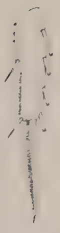
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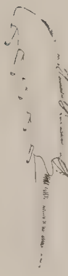
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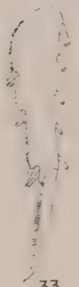
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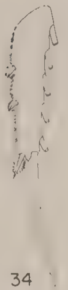
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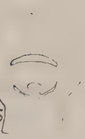
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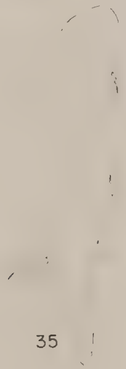
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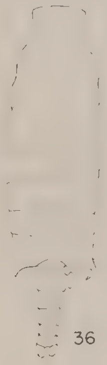
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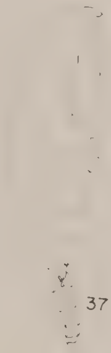
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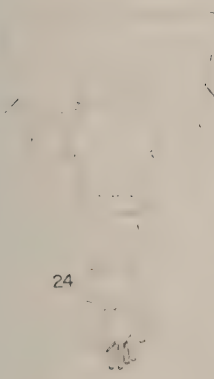
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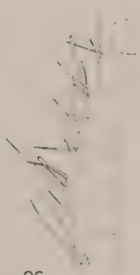
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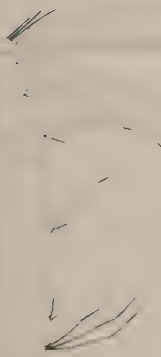
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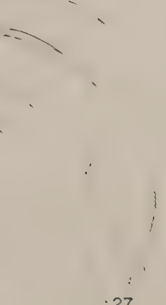
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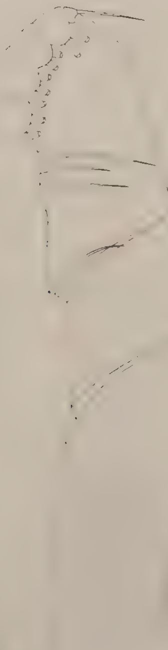
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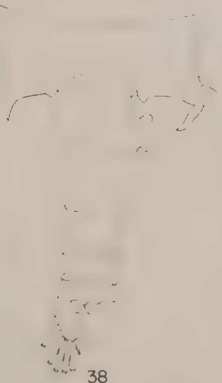
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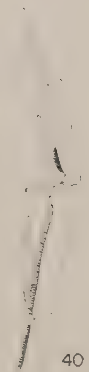
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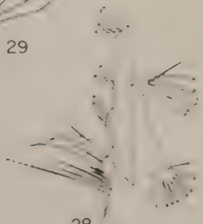
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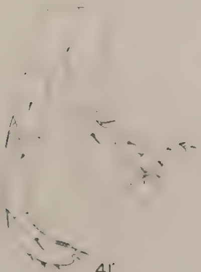
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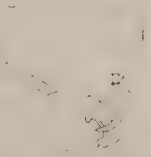
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ternal furcal setae. It can be distinguished from *C. cheirura* by the asymmetry of the abdomen in dorsal view and by the presence of dorsal tubercles on the anal segment. The female resembles *C. armata* Boeck (as described by G. O. Sars, 1903) in having an asymmetrical second abdominal segment. It can be distinguished from this species by the extremely large genital protuberance, the ventral lobe of the second abdominal segment extending to the left rather than to the right, the dorsal tubercles on the anal segment, and details of the fifth feet.

The geniculate antenna of the male *C. pofi* resembles that of *C. armata* Boeck (as described by Sars, 1903), *C. bradyi* and *C. discaudata* A. Scott, *C. bipinnata* Giesbrecht, and *C. cheirura* Cleve in having segments 17, 18, 19, and 20 separate and in having coarse, unequal pigmented teeth on segment 18. *C. pofi* can be distinguished from *C. bradyi* and *C. discaudata* by the produced right thoracic process. It can be distinguished from *C. armata, C. bipinnata,* and *C. cheirura* by the low, rounded genital process in lieu of the sharp spinous process in those species. The name of this species is derived from Pacific Oceanic Fishery Investigations.

Candacia guggenheimi new species

Figs. 22–41

LOCALITIES AND MATERIALS: 26° 25.2′ N., 155° 03.0′ W. (U. S. Fish and Wildlife Service "Hugh M. Smith" cruise 25, sta. 33, Feb. 10, 1954, 200–0 m. depth of tow, 2 females, 4 males); 32° 33′ N., 148° 51.5′ W. ("Hugh M. Smith" cruise 25, sta. 53, Feb. 22, 1954, 200–0 m. depth of tow, 1 male); 23° 56′ N., 157° 31′ W. ("Hugh M. Smith" cruise 30, sta. 112-1, Aug. 27, 1955, 140–0 m. depth of tow, 1 female); 21° 55′ N., 158° 08′ W. ("Hugh M. Smith" cruise 32, sta. 26, Feb. 5, 1956, 200–140 m. depth of tow, 1 female, 1 male); 0° 00′, 149° 38′ W. ("Hugh M. Smith" cruise 47, sta. 29, Oct. 27, 1958, 500 m. depth of tow, 1 female). This species has also been observed in samples collected at the following stations on "Hugh M. Smith" cruise 25 (all 200–0 m. collections): 21° 36.5′ N., 159° 00′ W. (sta. 2, Jan. 16, 1954); 33° 55.7′ N., 164° 58.5′ W. (sta. 11, Jan. 22, 1954); 26° 31′ N., 160° 00′ W. (sta. 26, Jan. 30, 1954); 22° 03.7′ N., 158° 40′ W. (sta. 29, Feb. 1, 1954); 29° 32′ N., 155° 04.8′ W. (sta. 35, Feb. 12, 1954); 32° 30′ N., 154° 59′ W. (sta. 37, Feb. 13, 1954). Physical, oceanographic, and other data for cruise 25 have been summarized by McGary and Stroup (1956) and that for cruise 30 by McGary, Jones, and Austin (1956).

Type material of *C. guggenheimi* has been deposited in the U. S. National Museum. A female from cruise 25, sta. 33, was selected as the holotype (USNM 102733). A male from this station was designated the allotype (USNM 102734). Paratypes are as follows: 1 female, 3 males, cruise 25, sta. 33 (USNM 102735); 1 male, cruise 25, sta. 53 (USNM 102736); 1 female, cruise 30, sta. 112-1 (USNM 102737); 1 female, 1 male, cruise 32, sta. 26 (USNM 102738); 1 female, cruise 47, sta. 29 (USNM 102739).

MEASUREMENTS: All measurements were made in the method described for the preceding species. The total length of five adult females ranges from 1.94 to 2.06 mm. The lengths and cephalothorax–abdomen ratios, based on three of these individuals are: holotype 2.01 mm., 2.9:1; paratypes 1.96 mm., 2.8:1; 2.04 mm., 3.1:1.

The total length of six adult males varies from 1.90 to 2.00 mm. These lengths and the

FIGS. 22–41. *Candacia guggenheimi* n. sp. 22, female, dorsal view; 23, female, lateral view; 24, fourth and fifth thoracic segments and abdomen, dorsal view, female; 25, genital segment, ventral view, female; 26, proximal seven segments of first antenna, female; 27, mandibular blade, female; 28, first maxilla, female; 29, second maxilla, female; 30, maxilliped, female; 31, third exopodal segment of first foot, female; 32, third exopodal segment of second foot, female; 33, third exopodal segment of third foot, female; 34, third exopodal segment of fourth foot, female; 35, fifth foot, female; 36, male, dorsal view; 37, male, lateral view; 38, fourth and fifth thoracic segments and abdomen, dorsal view, male; 39, fourth and fifth thoracic segments and genital segment, lateral view, male; 40, segments 17 through 19, right first antenna, male; 41, fifth feet, male. Figures 22, 23, 27, and 34 drawn from paratype; Figures 24–26, 28–33, and 35 drawn from holotype. Figures 36–39 and 41 drawn from allotype; Figure 40 drawn from paratype.

cephalothorax–abdomen ratios, based on four of these, are: allotype 1.90 mm., 2.91:1; paratypes 1.92 mm., 2.9:1; 1.94 mm., 2.7:1; 2.00 mm., 2.7:1.

DESCRIPTION: The general shape of the adult female is similar to other species of the genus *Candacia*. The head is truncate in dorsal view; thoracic segments 4 and 5 are fused and produced posteriorly into two symmetrical points (Fig. 22). In lateral view (Fig. 23), a small hump is visible on the dorsal surface at the junction of the head and first thoracic segment.

The genital segment is slightly asymmetrical; the lateral swelling on the left side is smaller and somewhat more expanded than that on the right side (Figs. 24, 25). A single dorsal spine is present on each swelling. The abdominal segments and furca have the following proportions (based on holotype): 40, 26, 19, 15 = 100.

The first antennae, when held against the body, reach to about the tips of the furcal rami. The proximal part of the antenna is thickened and consists of seven segments (Fig. 26). Segments 1 through 6 and 8 through 12 have one spine. There are indications that additional segments are furnished with a spine but no perfect antennae were present among the specimens examined.

The second antennae are similar to those of other species of *Candacia*. Basipodal segments 1 and 2 have one seta. Segment 2 of the endopod ends in two lobes. The outer lobe has six large and one small setae. The inner lobe has five large and one small setae and one minute seta proximad of the small one.

The exopod of the mandible apparently consists of four segments, the first three of which are furnished with a single seta. The terminal segment has two setae. The endopod is composed of one segment which is provided with six setae. The basal tooth of the mandible is furnished with two subequal points and a marginal point (Fig. 27).

The first maxillae are best described by reference to Figure 28.

The second maxillae are of large size (Fig. 29). The basal segment has four lobes. There are three long and one very short setae on the first lobe, one long and one short seta on the second lobe, one long and one short spine on the third lobe, and one long and one short spine on the fourth lobe. The second basipod segment has two subequal spines, the proximal one has a minute spine at its base. The endopod is furnished with three spines, the middle of which is slightly longest. In addition there are three bristles on the terminal part of the endopod.

The maxillipeds (Fig. 30) are small. The first basal segment is more than twice as long as the second basal segment. The former has one seta at a point about two-thirds of the segment length from the proximal end and two setae on the distolateral corner. The second basal segment is furnished with three unequal setae and one other seta on the apparent apex. Hair is present on the internal margin of this segment. The five endopodal segments are each furnished with one long and one short seta. The long seta on the terminal segment is somewhat longer than those on the other endopodal segments.

The third exopodal segments of swimming feet 1 to 4 are shown in Figures 31–34. The relative lengths of these segments to their respective terminal spines are as follows (based on several specimens): 1:1, 1:0.8 (estimate), 1:0.6, and 1:1.

The fifth feet are symmetrical and each terminates in one long stout finger and one short spinous process (Fig. 35). The former is about three times longer than the latter. The finger has several rounded serrations distally, and the spinous process is finely serrate. The external margin of the segment has two spinous processes. The internal margin bears two subequal setae in all observed specimens except one ("Hugh M. Smith" cruise 47, sta. 29-1) which has three internal setae on one foot.

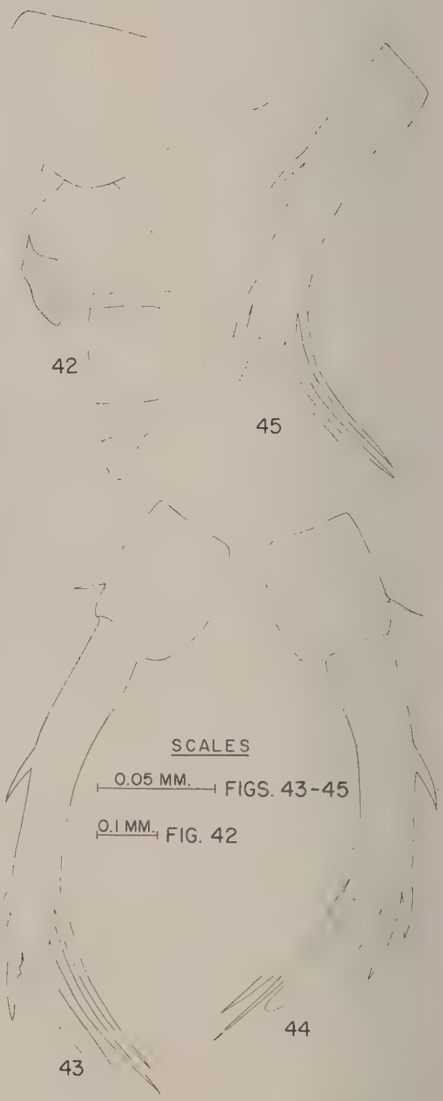
The following appendages of the preserved holotype are pigmented: the distal 18 segments of the first antennae, the distal spinelike claw on the first inner lobe of the first maxillae, portions of the first basipod segment and the distal five spines of the second maxillae, basipodal segments 1 and 2 of the first four pairs of swimming feet, and the terminal finger and spinous process of the fifth pair of feet. The female collected on "Hugh M. Smith" cruise 47, sta. 29, has additional pigmentation as follows: the distal 20 segments of first antennae, the spines on lobes 3 and 4 of the second maxillae, much of both rami of swimming feet 1 to 4 including several setae on the second and third exopodal segments and second endopodal segment, and the first basipodal segment of the fifth pair of feet.

The adult male (Figs. 36, 37) is slightly smaller than the female. The right posterior lateral process of the fifth thoracic segment is produced posteriorly and curved inward in dorsal view (Fig. 38). It reaches to the middle of the protrusion on the genital segment. In lateral view, the thoracic process has a decided upward bend (Fig. 39). The genital segment has a bilobed protrusion arising from near the posterior end of the right margin (Fig. 38). The abdominal segments and furca have the following ratios (based on three specimens): 22, 24, 20, 13, 9, 12 = 100.

Segments 17, 18, 19, and 20 of the right first antenna (Fig. 40) are separate, with 17, 18, and 19 toothed. The nearly uniform teeth on segment 18 are coarser than those on segments 17 and 19. The fifth feet are shown in Figure 41.

The following body parts and appendages of the male are pigmented (based on examination of several specimens): segments 17 to 25 of the right antenna, the distal 17 segments of the left antenna, the process on the right corner of the fifth thoracic segment, the clawlike spine on the distal part of the first inner lobe of the first maxillae, portions of the first basipod and spines on lobes 3 and 4 and the five large distal spines of the second maxillae, basipodal segments 1 and 2 of swimming feet 1 to 4.

REMARKS: The female of *C. guggenheimi* superficially resembles *C. longimana* Claus. The spines on the dorsal surface of the genital segment, the structure of the fifth pair of feet, and the somewhat smaller size of this species readily distinguish it from *C. longimana*. The bilobed protrusion on the genital segment and the structure of the fifth feet serve to distinguish the male. This species is named for the late Simon Guggenheim, one of the founders of the John Simon Guggenheim Memorial Foundation.



FIGS. 42–45. *Candacia truncata* (Dana). 42, fourth and fifth thoracic segments and abdomen, left lateral view, female, showing cement mass attached to genital segment; 43, 44, unlike fifth feet, female, from same specimen; 45, fifth foot, female, with serrated external spinous processes, from another specimen.

NOTES ON TWO OTHER SPECIES

Candacia truncata (Dana)
Figs. 42–45

Candace truncata Dana, 1849, Proc. Amer. Acad. Arts Sci., 2: 24.

Candacia truncata Giesbrecht and Schmeil, 1898, Das Tierreich, 6, p. 130; auct.

Candacia turgida Wilson, 1950, U. S. Natl. Mus. Bul. 100, 14(4): 183–184. New synonomy.

In the course of examining plankton samples we have encountered numerous individuals of a species which appears to agree with the description of *C. turgida* Wilson (1950). We believe, however, that these specimens, as well as *C. turgida,* are identical with *C. truncata* (Dana).

The pigmented process on the ventral side of the female genital segment (shaded portion of Fig. 42), which Wilson considered to be a protrusion of that segment, appears to be a mass of cement associated with a spermatophore. In most of the samples examined there were some females with this mass and others without. Furthermore, the mass can be removed quite easily with a needle. Tanaka (1935) presented a figure of a female *C. truncata* showing such a mass adhering to the genital segment.

Wilson's figure of the female fifth feet (1950: pl. 22, fig. 308) of his *C. turgida* apparently is not complete in detail. Dr. Thomas E. Bowman has kindly sent us a sketch of the fifth feet from one of the syntypes of this species. His sketch and the numerous fifth feet examined from our material agree in the structure of the large terminal finger. The external margin of this finger in all specimens examined and in Dr. Bowman's sketch is finely serrate along most of its length. The distolateral and two external spinous processes are, however, somewhat variable. In some specimens the distolateral spinous process has one or two relatively large teeth on the internal margin as figured by Giesbrecht (1892). One has a single external tooth opposite two internal ones; another has seven small internal teeth. In some specimens the feet are asymmetrical, being unequal in length and with unlike dentition on the distolateral spinous process. One specimen has four teeth on one foot and two on the other. In yet another, this process is toothed on one foot and smooth on the other. Figures 43–45 show some of the variations of the fifth feet of the female *C. truncata* from the central Pacific. Typical males of *C. truncata* have also been observed in our collections. Specimens of this species were obtained in the following localities: 22° 03.7′ N., 158° 40′ W. ("Hugh M. Smith" cruise 25, sta. 29, Feb. 1, 1954, 200–0 m. depth of tow); 0° 00′, 149° 36′ W. ("Hugh M. Smith" cruise 47, sta. 30, Oct. 27, 1958, surface collection). Seven females from 23° 55′ N., 157° 31′ W. ("Hugh M. Smith" cruise 30, sta. 112-2, Aug. 27, 1955, 49 m. depth of tow) have been deposited in the U. S. National Museum (USNM 102740).

Candacia norvegica (Boeck)
Figs. 46–65

The distribution of *Candacia norvegica* (Boeck) in the North Atlantic has been summarized by Farran (1948). Sewell (1932) described a variety *tropica* from the Indian Ocean. In his reports on the Carnegie and Albatross collections, Wilson (1942, 1950) recorded *C. norvegica* from many stations in the tropical and temperate Pacific Ocean. In a

FIGS. 46–65. *Candacia norvegica* (Boeck). Figures 46–62 refer to Pacific specimens; Figures 63–65 to Atlantic specimen. 46, female, lateral view; 47, abdomen, dorsal view, female; 48, lateral view of left genital spinous process; 49, lateral view of right genital spinous process; 50, 51, mandibular blades from one individual female, showing unlike basal teeth; 52, first maxilla, female; 53, second maxilla, female; 54, fifth feet, female, with two external spinous processes on each foot; 55, fifth feet, female showing three external spinous processes on one foot and two on the other; 56, male, dorsal view; 57, male, lateral view; 58, fourth and fifth thoracic segments and abdomen, dorsal view, male; 59, genital segment, ventral view, male; 60, fourth and fifth thoracic segments and genital segment, right lateral oblique view, male; 61, segments 17 through 19, right first antenna, male; 62, fifth feet, male; 63, abdomen, dorsal view, female; 64, left genital spinous process; 65, right genital spinous process. Figures 47–49 and 54 are from Pacific female 2.96 mm. total length; all others of Pacific female are from specimen 2.80 mm. total length.

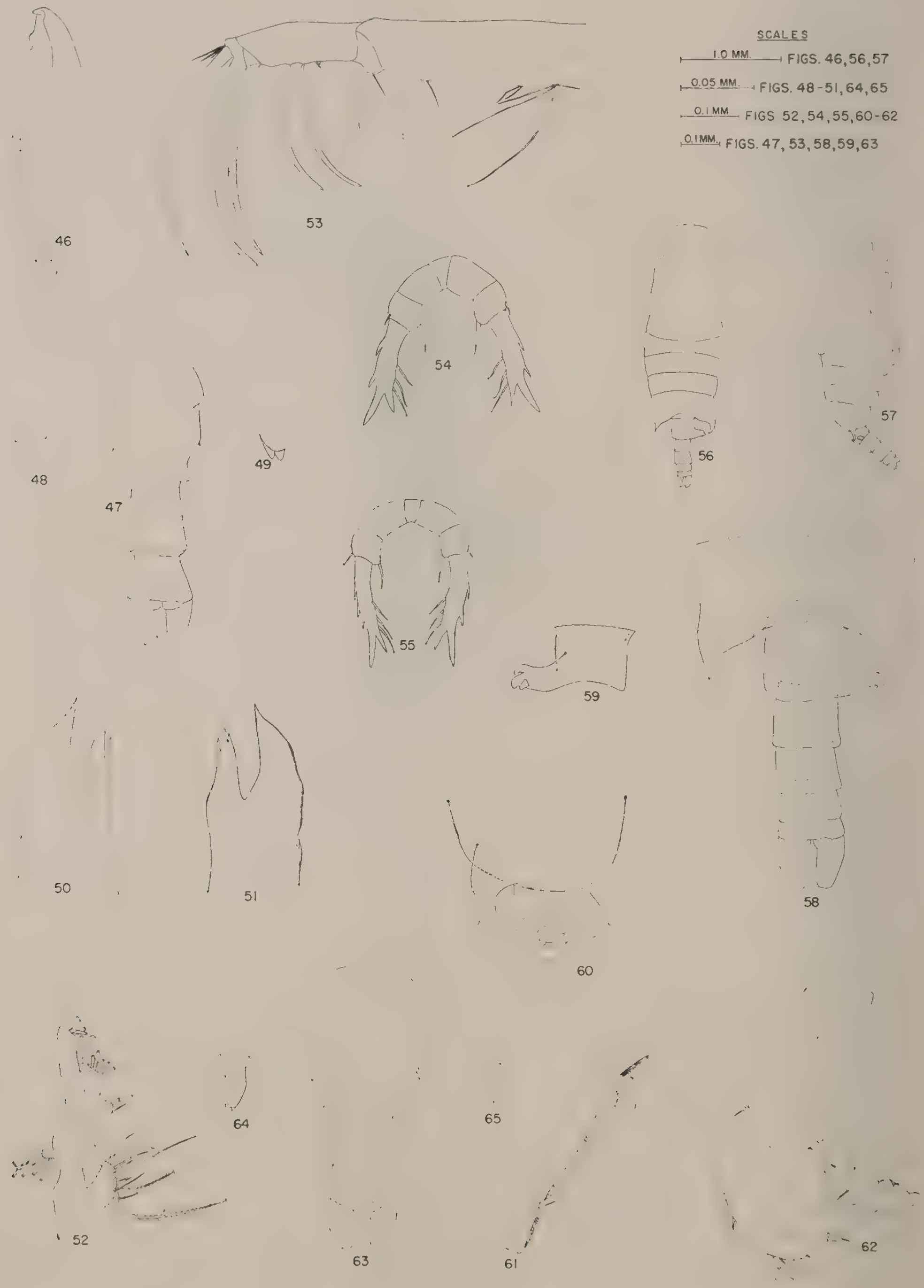

SCALES
1.0 MM. FIGS. 46, 56, 57
0.05 MM. FIGS. 48-51, 64, 65
0.1 MM FIGS 52, 54, 55, 60-62
0.1 MM. FIGS. 47, 53, 58, 59, 63

TABLE 2

COMPARISON OF FEMALE *Candacia norvegica* FROM GEORGES BANK, THE PACIFIC, AND VARIETY *tropica*

SOURCE	TOTAL LENGTH* (mm.)	CEPHALOTHORAX–ABDOMEN RATIO*	ABDOMEN RATIO = 100 SEGMENT NUMBER			
			1	2	3	Furca
Georges Bank (USNM)	3.24	2.89:1	45	24	18	13
Pacific	2.96	2.66:1	45	24	17	14
Pacific	2.80	2.83:1	44	22	19	15
Variety *tropica* (Sewell, 1932)†	2.28	2.92:1	43	25	19	13

* Includes telescoped portion of abdominal segments of the specimens from Georges Bank and from the Pacific. Sewell's data used for *tropica*.

† Sewell apparently reversed the figures for the ratio of the anal segment and furca. Measurement of his figure of the abdomen shows that the length of the anal segment exceeds that of the furca.

recent paper, Fleminger and Bowman (1956) have reported that Wilson's determinations were incorrect and that *C. norvegica* was not present in any of the Carnegie and Albatross material in the U. S. National Museum. The only other mention of this species from the Pacific appears in Tanaka's (1953) list from the Izu region off southern Japan. Because no description or figures have been given of Pacific specimens and because of the apparent rarity of the species in that ocean, we are including a description based on two females and one male collected in the central North Pacific. These specimens were collected at 37° 43.9′ N., 165° 0.5′ W. ("Hugh M. Smith" cruise 25, sta. 13, Jan. 24, 1954, 200–0 m. depth of tow, 2 females and 1 male) and have been deposited in the U. S. National Museum (USNM 102741).

We have compared our specimens with Atlantic *C. norvegica* collected south of Georges Bank (northwest Atlantic) and loaned to us by the U. S. National Museum, with Sewell's description of *tropica*, and with Sars' (1903) redescription of *C. norvegica* based on specimens from the Norwegian Sea. Differences in the details of the lateral spines of the female genital segment were found. Sars implied in his description that these spines are simple and single pointed. Variety *tropica* Sewell is stated to have bifid spines on both sides. Our Pacific specimens agree with *tropica* in this respect, but the spines are somewhat smaller (Figs. 48, 49). The Georges Bank specimen examined by us has a slightly bifid tip on the left spine and a simple spine on the right (Fig. 64). Furthermore, Sars stated that the genital segment is perfectly symmetrical, but in the specimens from the Pacific (Fig. 47) and Georges Bank (Fig. 63) and in *tropica*, the left spine is larger than the right. We believe that the size and detail of these spines is variable and may be of little diagnostic value. Table 2 gives the total length, cephalothorax–abdomen ratio, and abdominal segment ratios of the specimen from Georges Bank, Pacific specimens, and Sewell's variety *tropica*.

The structure of the female fifth feet presents some variation among specimens from the Pacific and Georges Bank, Sewell's *tropica*, and Sars' description. Sewell stated that the fifth feet of *tropica* were unlike *norvegica* in that there are two rather than three "spines" on the outer margin of the distal segment, but Sars (1903) mentioned that this margin may have two or three small "denticles." Of our two Pacific specimens, one has two spinous processes on each foot (Fig. 54), and the other has two on one foot and three on the other (Fig. 55). The Georges Bank specimen has two outer spinous processes on each foot. It appears that this is a variable characteristic. In *tropica* the two terminal fingers of the fifth feet are equal, but in all others examined or described the length of the outer is about twice that of the inner finger.

Sars stated that the points on the corners of the fifth thoracic segment diverge in dorsal view, but in all other specimens and descriptions examined by us these points point straight caudad.

The male from the Pacific (Figs. 56–62) agrees closely with the Georges Bank specimen and with the description given by Sars. The total length of our specimen is 2.68 mm. and that of the Atlantic specimen is 3.23 mm.

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Contributions to the Knowledge of the Alpheid Shrimp of the Pacific Ocean

Part VI. *Prionalpheus,* a New Genus of the Alpheidae

ALBERT H. BANNER and DORA MAY BANNER

Reprinted from PACIFIC SCIENCE
July, 1960

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Contributions to the Knowledge of the Alpheid Shrimp of the Pacific Ocean

Part VI. *Prionalpheus,* a New Genus of the Alpheidae[1]

ALBERT H. BANNER and DORA MAY BANNER[2]

IN THE EXTENSIVE collections of shrimp upon which this series of papers is based, there are three fragmentary specimens in which the mouth parts are entirely unlike those of any other genus of the family Alpheidae. These are of two species but, because of the fragmentary condition of the specimens, only one of the species is named. The specimens were collected in Fiji and the Society Islands while the senior author was there under a grant from the Bernice P. Bishop Museum, Honolulu. The study has been supported by grants from the National Science Foundation (NSF–G 1754 and NSF–G 3863).

Prionalpheus gen. nov.

DIAGNOSIS: Body form usual, similar to *Alpheopsis;* rostrum present and small; supra-, extra-, and infracorneal teeth lacking; anterior carapace projecting to cover corneas from dorsal and lateral view, flat, not inflated to form orbital hoods; antennules and antennae normal for family; mandibles without a trace of molar process, incisor process greatly expanded and consisting of five strong teeth, the most anterior tooth of left mandible developed as an awl-shaped process that slides within almost closed tube formed by corresponding portion of right mandible; maxillulae with middle lobe moderately or greatly expanded, inner lobe bearing strong spines; maxillae reduced in size, endites greatly reduced, palp present, scaphognathite relatively small and narrow; first maxilliped with endite large and rounded, endopod without apparent segmentation, exopod well developed but without any basal exite, epipodites present; second maxilliped with basal article of endopod apparently united with basipodite and large, next article somewhat to greatly reduced, penultimate article not greatly expanded and ultimate article rounded in outline rather than short and laterally expanded; third maxillipeds not markedly different from those of other genera; only one cheliped known, similar in form to those of *Alpheopsis equalis* Coutière; second legs with carpus divided into three or four articles; following legs slender, elongate with biunguiculate dactylus; pleura of sixth abdominal somite articulated; telson and uropods normal; no anal tubercles; branchial formula apparently including five pleurobranchs, no arthrobranchs, and epipodites only on first and second maxilliped.

TYPE SPECIES: *Prionalpheus triarticulatus,* described below.

DISCUSSION: Even without both chelae of the first pair, there can be no doubt that this genus belongs to the family Alpheidae. This is shown by the development of the sole chela on the first walking legs and the chelate second legs with a multiarticulate carpus, by the whole body form, by the development of the carapace to cover the orbits of the eyes, by the development of the antennules and antennae, as well as by less important characteristics like the form of the third legs, the development of articulated pleura of the sixth abdominal segment, and the form of the telson and uropods. If it were not for the unique development of the mouth parts, these species would fall into the genus *Alpheopsis* without modification of the generic description.

However, no mouth parts like these have been described for any species of any genus of the family. In Coutière's thesis (1899: 153–173) the mouth parts of the members of the family were shown to have little variation, with the possible exception of the third maxilliped. No subsequent publication has shown any greater differences in the inner mouth parts, although

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[1] Contribution No. 132, Hawaii Marine Laboratory. Manuscript received November 1, 1958.

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Chace did erect a new genus *Pomognathus* (1937: 124, fig. 5) on the basis of a species with an expanded third maxilliped. In *Prionalpheus* the differences lie principally in the overdevelopment of the incisor process portion of the mandibles, with the corresponding loss of the palp and molar portion, and in the seemingly primitive condition of the second maxilliped, which, although it has coalescence of some of the articles, assumes a form more reminiscent of the maxilliped of Mysidacea than those of most other Decapoda. The development of the maxillulae differs in the two species, and the modification of the maxillae and of the first and third maxillipeds are not as striking. The inclusion of this genus within the family Alpheidae will necessitate changes in its definition as given by Coutière ("Mandibles toujours profondément bipartites, 'palpe' à deux articles. . . ." 1899: 322).

As stated above, except for the development of the mouth parts, this genus is most similar to *Alpheopsis* within the family. Of course, without the chelae it is difficult to decide where its affinities lie, but even if they were present and similar to those of *Alpheopsis* as they are expected to be, it would still be difficult to assign this genus to any phylogenetic scheme for the family. It is generally accepted that *Athanas* is the most unmodified genus, and *Alpheus* and *Synalpheus* the most highly modified, on the basis of both the orbital hoods and development of the large chela; such a scheme would leave *Alpheopsis* in an intermediate position. However, *Prionalpheus,* intermediate in most characteristics, is not intermediate in the modification of the mouth parts.

The species of *Alpheopsis* available in the collection, including *Alpheopsis equalis* Coutière, *A. diabolus* Banner, and *A. tetrarthri* Banner, have been re-examined to determine if they have this modification of mouth parts. They do not. However, two species described by Coutière, A. *idiocarpus* and *A. fissipes* (1908:4), should also be re-examined; *A. idiocarpus* especially appears to be similar to *P. triarticulatus.*

It is unfortunate that the specimens were so few in number, because a number of characteristics should be investigated more thoroughly by dissection. For example, the origin of the peculiar tooth on the ventral side of the body at the base of the antennules should be studied; the branchial formula should be determined more carefully; the mouth parts of the right side should be compared to those of the left. With only three specimens representing two species, it was decided to leave the specimens intact for future workers.

Little can be said of the distribution of these species. All three were collected from the usual collecting site for snapping shrimp, the reef flat and the outer portion of the reef, in Fiji and Tahiti. No special niche or commensal association was noted for them, yet these three specimens were the only ones found in all of the collecting trips to similar habitats in these and other islands, collections that produced about eight thousand specimens. Presumably, these species must have special environmental requirements, but what the requirements may be we cannot say.

The generic name is derived from the Greek, *prionos,* meaning "saw"; the gender is masculine, as it is in *Alpheus.*

KEY TO THE SPECIES

Carpus of second legs with three articles; only scattered setae on terminal article of third maxillipeds, these not reaching over half the length of that article.................................... ....*Prionalpheus triarticulatus*

Carpus of second legs with four articles; terminal article of third maxillipeds bearing numerous setae equal in length to that article............. ....*Prionalpheus* species

Prionalpheus triarticulatus sp. nov.

Fig. 1

TYPE AND ONLY SPECIMEN: A 10.7 mm. nonovigerous female (3.9 mm. carapace length) collected in middle of reef flat on fringing reef, Korolevu, Vitilevu, Fiji, by senior author, 17 March 1954 (BF-13).

DESCRIPTION: Rostrum triangular, base demarked from adjacent margin of carapace, tip acute, reaching to end of first antennular article, and bearing four short setae; dorsal surface with slight carina. Anterior carapace obscuring eyes from dorsal and lateral views, but not form

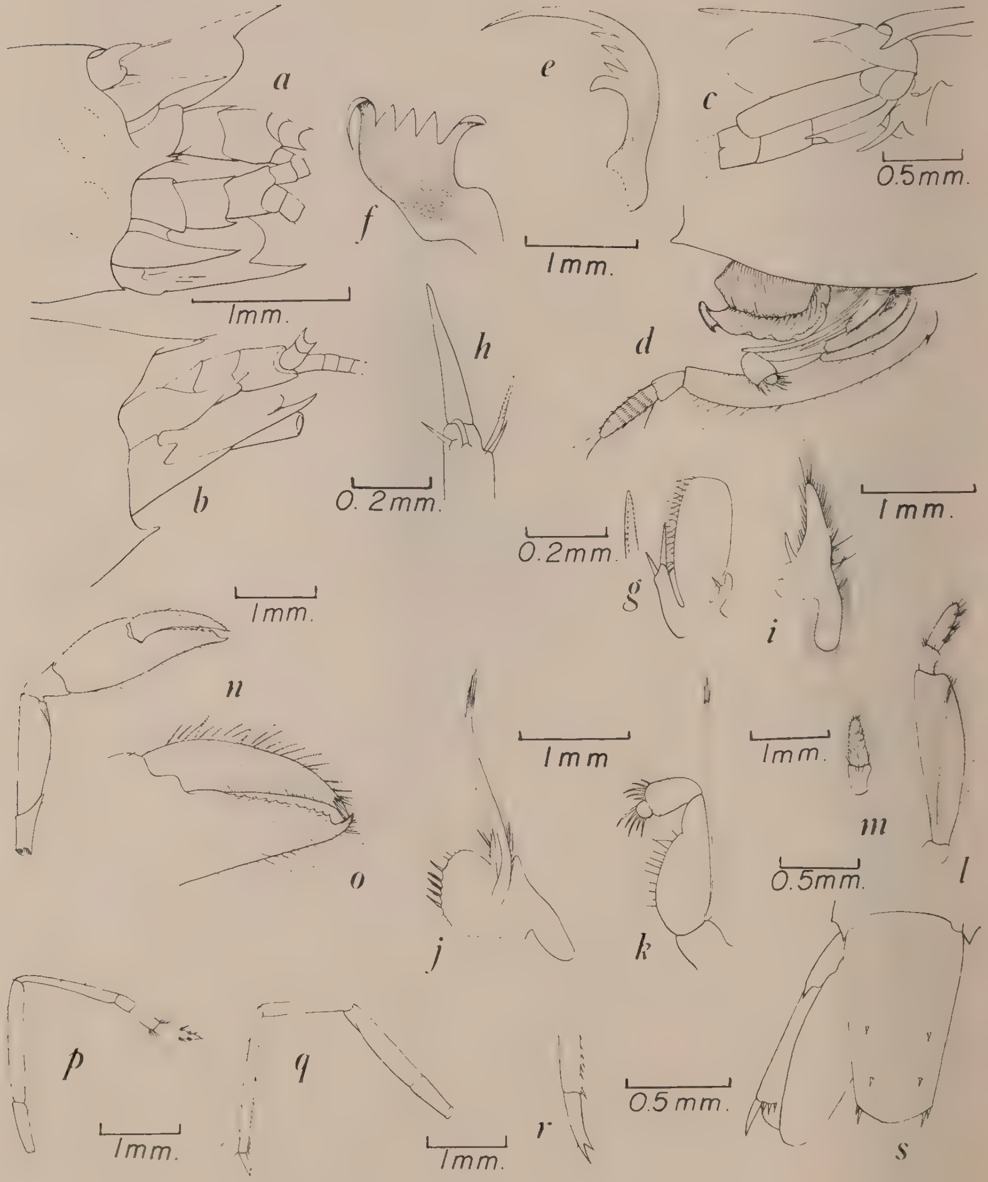
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FIG. 1. *Prionalpheus triarticulatus* Banner. *a, b,* Anterior body region; *c,* base of antenna and antennules, in situ, ventral view; *d.* mouth parts of right side, medial view, showing groove on anterior end of mandible; *e,* left mandible, posterior view; *f,* left mandible, medial view; *g,* first maxilla, with enlargement of teeth on bristle; *h,* first maxilla, inner lobe, side opposite of *g; i,* second maxilla; *j, k, l,* first, second, and third maxillipeds; *m,* distal articles, inner face, third maxilliped; *n,* chelipeds, lateral view; *o,* fingers of chela; *p,* second legs; *q,* third legs; *r,* third leg of dactylus; *s,* telson and uropods.

ing swollen orbital hoods; without trace of ocular teeth; pterygostomial tooth produced and acute.

Basal articles of antennules short and heavy, with second article slightly broader than long; lateral spine of stylocerite strong, with tip reaching slightly beyond end of second antennular article. Ventral lateral tooth of basicerite heavy, acute, and curving under scaphocerite; superior lateral margin of basicerite projecting as a rounded lobe; scaphocerite with strong lateral spine, slightly curved towards tip, and reaching beyond end of antennular peduncle, squamous portion broad and anteriorly rounded, reaching to end of antennular peduncle; carpocerite equal in length to antennular peduncle. Either basal article of antennules or of antennae, or sclerite at their bases on ventral side of head bearing a sharp, acute tooth (see Fig. 1*c*).

Mouth parts protrudent and conspicuous in lateral view. Mandible large, curved distally and flattened laterally, bearing five teeth; posterior tooth acute, longer than middle teeth and curved; three middle teeth strong, acute, and of equal size; anterior tooth of left mandible awl-shaped, curved, almost 4 times the length of middle teeth and fitting into almost closed groove developed by corresponding tooth of right mandible; no trace of palp or *pars molaris*. Maxillulae with middle lobe greatly expanded, 2.2 times as long as broad, exceeding the inner lobe by 0.7 of its length, distally truncate with rounded corners, and bearing two series of setae on inner margin; inner lobe short, obliquely truncate, and bearing strong terminal spine almost as long as article and four other shorter spines, one curved; outer lobe smaller than inner and bearing a single weak spine. Maxillae reduced in size with total length of scaphognathite equal to length of maxillule; endites reduced to small lobes; palp without segments and bearing only few setae; setiferous scaphognathite narrow, with posterior lobe only 2 times as long as broad. First maxilliped with endite rounded, solitary (unless basal endites were lost in dissection), bearing four strong articulated spines and a few setae; endopod with no apparent segmentation, bearing few setae; exopod well developed; epipodite well developed, lobelike, rounded. Second maxilliped apparently with only four articles distal to articulation of exopod; basal article of endopod with maximum length twice the breadth, inner margin bearing strong spines; next article with maximum length 0.7 that of basal article; penultimate article broader but shorter than preceding article, bearing setae; ultimate article half as broad and one-quarter as long as penultimate, bearing five strong articulated spines. Third maxillipeds normal for family, with ultimate article twice length of penultimate, 0.3 length of basal article, and bearing few short scattered setae along margins.

Only one of first pair of legs present. Ischium 0.3 length of merus; merus 4 times as long as broad, unarmed; bearing few scattered setae; carpus somewhat cyathiform, distally expanded to accommodate base of propodus; palm slightly shorter than fingers, 0.7 as long as broad, somewhat compressed; fingers heavy, fixed finger bearing fine serrations, dactylus with straight cutting edge, free margin armed with setiferous bristles; tips of fingers crossing.

Second legs with merus 7 times as long as broad; three articles of carpus with ratio 10:2:3, first article 0.8 as long as merus, twice as wide distally as proximally; fingers and palm of chela subequal, together 1.4 times as long as distal article.

Third legs with ischium 0.4 length of merus, bearing three setae; merus 5 times as long as broad, unarmed; carpus 0.9 as long as merus, also unarmed; propodus 1.4 times length of merus, about 15 times as long as broad, armed with short, very fine spines and setae along inferior margin; dactylus biunguiculate, with inferior unguis the heavier and shorter.

Telson 2.8 times as long as broad distally, 1.5 times as broad proximally as distally, sides with uniform taper, tip broadly arcuate, dorsal and terminal spinules small. Uropods narrow; tooth on proximal article small; distal tooth on outer uropod heavy, flanked by three smaller teeth.

DISCUSSION: The origin of the spine on the ventral side of head could not be ascertained without dissections which would ruin the type specimen. It appears to arise from an inner portion of the base of the antennae.

This species will be contrasted to *Prionalpheus* species under that form. It is superficially similar to *Alpheopsis idiocarpus* Coutière, a species that may be found to be in this genus when it is re-examined; the two species differ, however, even if the mouth parts should be found to be similar, in the biunguiculation of the dactylus of the third leg. *Alpheopsis fissipes* Coutière, which may also be found to belong in this genus, differs in the number of articulations of the carpus of the second legs.

The specific name refers to the number of articles of the carpus of the second leg.

Prionalpheus sp.

Fig. 2

LOCALITIES: 1 female, nonovigerous, carapace length 2.8 mm., total length 5.6 mm., from Arue, Tahiti, in dead coral heads 5–10 ft. deep (BD-3); 1 ovigerous female, carapace length 3.7 mm., total length 10.6 mm., from outer edge of fringing reef at Korolevu, Vitilevu, Fiji (BF-16); both collected by senior author. Tahitian specimen with one second and one third leg intact; Fijian specimen with only second legs intact.

DESCRIPTION: Base of rostrum not demarked from curvature of anterior margin of carapace, tip of rostrum reaching to middle of first antennular article and bearing four setae; pterygostomial angle somewhat produced and acute, but not projecting as a definite tooth.

Antennular peduncle short and heavy, with second article about as long as broad; stylocerite reaching almost to end of second antennular article; outer flagellum bearing numerous heavy, but not stiff, setae. Ventral lateral spine of basicerite acute but shorter than that of *P. triarticulatus;* dorsal lateral lobe present; lateral spine of scaphocerite reaching to middle of third antennular article, rounded edge of squamous portion to end of second article; carpocerite reaching to end of antennular peduncle. No ventral spine anterior to labrum at bases of antennules or antennae.

Left mandibles similar to that of *P. triarticulatus* except anterior awl-shaped tooth only twice as long as adjacent tooth, and posterior tooth not acute but rounded; anterior process of left mandible fitting into corresponding groove of right mandible. Maxillulae of more normal form, as shown in Figure 2*e*; inner lobe bearing numerous strong, hooked setae. Maxillae similar in form to those of *P. triarticulatus,* but with posterior portion of scaphognathite more slender. First maxilliped with curvature of endite less uniform; exopodite bearing laterally a heavy setiferous bristle (broken in specimens); epipodites greatly reduced. Second maxilliped with endopod composed of only three conspicuous articles, one being very short and sandwiched between the first and third; basal article more rectilinear than that of *P. triarticulatus;* penultimate article pear-shaped in outline, about 1.3 times as long as maximum breadth, bearing numerous heavy spines; tip half-round in outline, bearing six strong spines. Third maxillipeds similar in conformation to those of *P. triarticulatus* but with all three articles of endopod bearing heavy setae, the setae of last article being equal in length to article.

First legs lacking on both specimens. Carpus of second legs with four articles bearing the ratio 10:2.6:1.8:4.4; chela somewhat longer than distal carpal article, fingers and palm subequal. Third legs with ischium unarmed; merus 4 times as long as broad; carpus 0.9 as long as merus; propodus 1.2 times as long as merus, armed distally with few weak spines; dactylus biunguiculate.

Telson 2.1 times as long as posterior margin is broad, 1.2 times as broad anteriorly as posteriorly, lateral margins almost straight, posterior margin strongly arcuate; only one pair of dorsal spinules, located posterior to middle; inner pair of spines at posterior lateral margin half as long as posterior margin is broad. Only one tooth on basal article of uropod; distal shoulder of outer uropod armed with one strong lateral spine and three flanking spines each almost as long as lateral spine.

DISCUSSION: Even without the first legs, these specimens may be distinguished with ease from *P. triarticulatus.* Among more readily apparent differentiating characteristics, this species has (1) margins of the rostrum which are confluent with the anterior margin of the carapace;

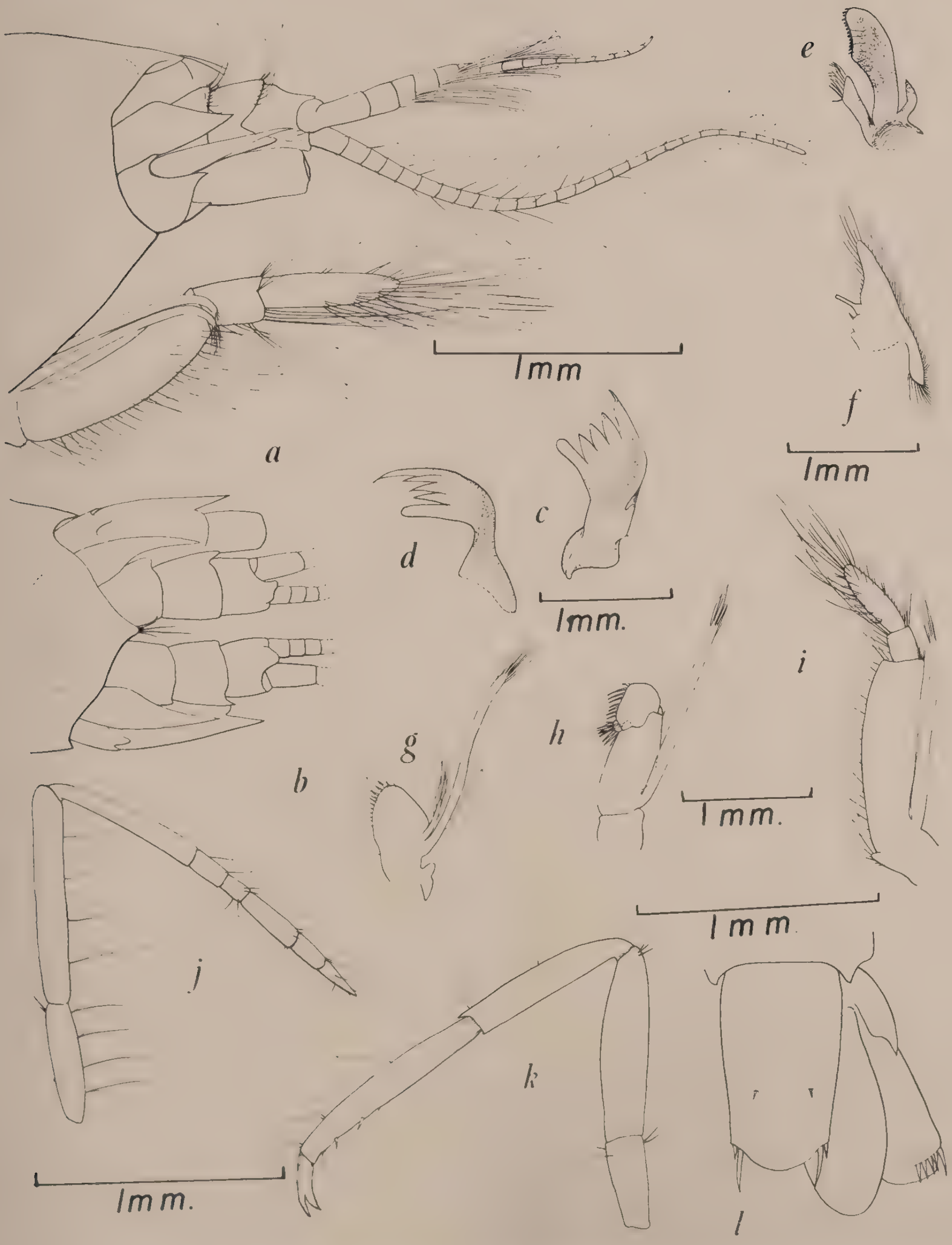
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FIG. 2. *Prionalpheus* sp. *a. b.* Anterior body region; *c. d,* left mandible, median and posterior views; *e, f.* first and second maxillae; *g. h. i.* first, second, and third maxillipeds; *j.* second legs; *k.* third legs; *l.* telson and uropods.

(2) a pterygostomial angle which is less pronounced; (3) shorter scaphocerites and ventral lateral teeth of the basicerites; (4) more hirsute third maxillipeds; (5) four, rather than three, articles in the second legs; (6) a telson which has a different armature. In the mouth parts, the differences in form of the mandibles, the maxillulae, and the second maxillipeds are striking, as can be seen by comparing the figures. Whether the differences in length of the stylocerites, in the form of the third legs, and in the armature of the telson and uropods are significant cannot be determined without more specimens.

The species has been left unnamed because the specimens are so incomplete.

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Contributions to the Knowledge of the Alpheid Shrimp of the Pacific Ocean

Part VII. On *Metabetaeus* Borradaile, with a New Species from Hawaii

ALBERT H. BANNER and DORA MAY BANNER

Reprinted from PACIFIC SCIENCE
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Part VII. On *Metabetaeus* Borradaile, with a New Species from Hawaii[1]

ALBERT H. BANNER and DORA MAY BANNER[2]

THE GENUS *Metabetaeus* was described by Borradaile (1898: 1014) to contain the species originally described by Whitelegge (1897: 147) as *Betaeus minutus*. These descriptions and Coutière's subsequent discussion of the genus (1899: 374) were all based on a series of specimens collected at Funafuti in the Ellice Archipelago. Nothing more on either the genus or the species was recorded until R. W. Hiatt collected additional specimens of the species in a brackish pond at Arno in the Marshall Islands (Banner, 1957: 193).

Since the publication of the 1957 paper, additional specimens belonging to this genus have been observed alive and collected. *M. minutus* was taken from two different islets on Jaluit in the Marshall Islands during a trip in April, 1958, to observe typhoon damage on that atoll. The trip was sponsored by the Office of Naval Research, the Pacific Science Board, and the Bernice P. Bishop Museum.

More interesting is a new species of the genus collected from one locality on the island of Hawaii. The first several specimens came to us from the collections of the Bishop Museum; they had been collected in a pool in the Ka'u district of Hawaii by E. H. Bryan, Jr., Marian Kelly, and William Meinecke. In February, 1958, we collected more specimens from this pool. Many other pools, both in the Ka'u district and in other areas on other islands, were investigated, but no more specimens of this species were seen.

This study was supported in part by the National Science Foundation Grant NSFG–3863. The authors wish to express their appreciation to Mr. William Meinecke, who guided them to the pool and aided in the capture of the specimens.

Metabetaeus lohena sp. nov.

Fig. 1

SPECIMENS: Type specimen, an ovigerous female 16.6 mm. long; paratypes, 5 specimens collected by the authors and 4 other specimens collected by Bryan, Kelly, and Meinecke.

TYPE LOCALITY: All specimens came from a pool in the base of the rock known to the Hawaiians as Lohena, a few hundred yards from shore between the deserted villages of Wai-o-ahu-kini and Ka'ili-ki'i, immediately west of Ka Lae or South Point on Hawaii. Lohena is a rock perhaps a hundred or more feet in diameter surrounded by the boulders of an a'a lava flow; in its base are several fissures, one of which is a cave about 30 ft. long, 10 or 12 ft. wide at the mouth and 15–20 ft. high; the pool of brackish water is 4–6 ft. deep in the bottom of the cave.

DESCRIPTION: Carapace rounded dorsally, without grooves or keels. Rostrum acute with tip reaching to middle of first antennular article; dorsal surface rounded, lateral margins posteriorly concave. Supraorbital spines acute, half as long as rostrum. Eyes completely concealed in dorsal and lateral aspects; pigmented portions of corneas greatly reduced. Pterygostomial margin rounded.

Cardiac notch wanting; pleura of sixth abdominal somite articulated.

Second article of antennular peduncle as long as broad, shorter than visible portion of first, and longer than third article; flagella about as long as carapace. Stylocerite acute, with tip reaching to end of first antennular article.

Basicerite with strong, acute tooth below articulation of scaphocerite. Scaphocerite with

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[1] Contribution No. 133, Hawaii Marine Laboratory.

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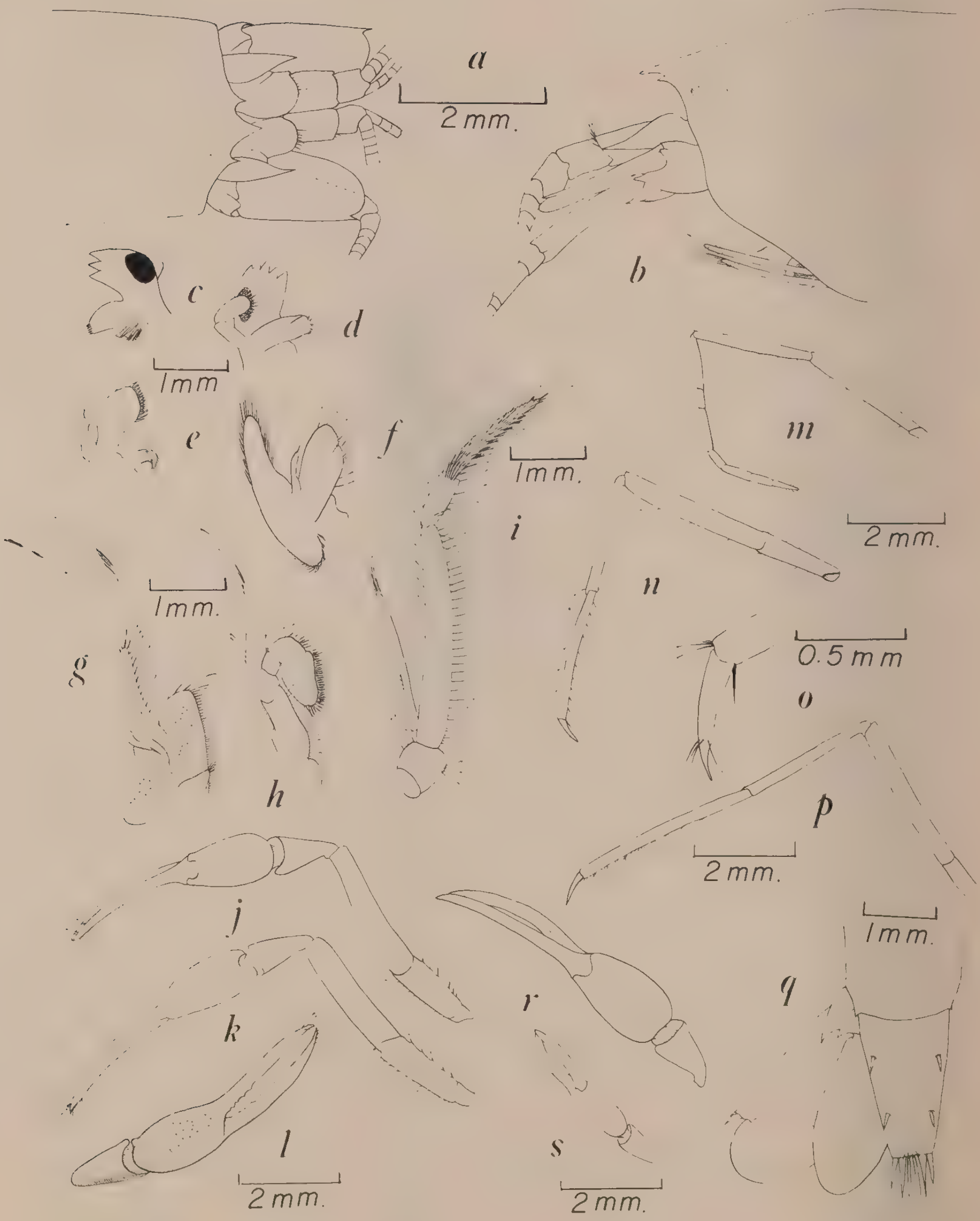
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FIG. 1. *Metabetaeus lohena* Banner. *a, b,* Anterior region, dorsal and lateral aspects; *c, d,* mandibles; *e,* first maxilla; *f,* second maxilla; *g,* first maxilliped; *h,* second maxilliped; *i,* third maxilliped; *j,* left chela, outer side; *k,* right chela, inner side; *l,* left chela, upper side; *m,* second leg; *n,* third leg; *o,* dactylus, third leg; *p,* fifth leg; *q,* telson and uropods; *r, s,* paired chelae of a nonovigerous 18.4 mm. female.

lateral tooth of moderate development, about equal in length to rounded portion; squamous portion reaching to end of antennular peduncle. Carpocerite slightly longer than both antennular peduncle and scaphocerite; flagellum somewhat longer than body.

Mandibles of normal form but bearing a large oval black spot on the body of the mandible; black spot with sharp margins and persistent even after preservation in alcohol. Maxillule with outer lobe without setae or spines, but with two heavy, thickened lobes, somewhat similar in form to a bottle opener. Other mouth parts showing only minor differences from those normal to the family.

Chelipeds symmetrical, enlarged. Ischium 3 times as long as broad, bearing on superior margin a row of short spines, on inferior margin a row of setae. Merus unarmed, 5 times as long as broad, slightly over twice length of ischium. Carpus subconical, proximally small in diameter, distally 3 times the proximal diameter; distal margins somewhat collarlike around base of propodus; articles without spines. Palm of chela somewhat inflated, subcircular in cross section, 1.6 times as wide at maximum diameter as long. Fingers long, slender, curved, 1.5 times length of palm; proximally both fingers armed with low, widely spaced teeth.

Second legs long and slender, ischium and merus equal in length and both about 10 times as long as broad. Sum of lengths of first three carpal articles equal in length to merus; ratio of the carpal articles is 10:3.5:8:3.5:5. Fingers of chela subequal in length to last carpal article, slightly longer than palm.

Third legs slender. Ischium unarmed, except for scattered setae, almost 4 times as long as broad. Carpus unarmed, 0.8 as long as merus, about 0.6 as broad. Propodus also slender, slightly curved, tapering very slightly distally, 1.1 times as long as carpus, and bearing 10 slender, fine spines along inferior margin. Dactylus simple, slender, acute, 0.2 as long as propodus.

Fourth and fifth legs similar to, but progressively longer, than third. "Brush" on propodus of fifth legs well developed.

Telson twice as broad at base as at tip, and 3 times as long as broad at tip; lateral and terminal margins almost straight; dorsal surface slightly convex. Spines heavy with medial pair of terminal spines about as long as tip is broad; lateral pair slightly shorter; middle portion of tip with small tuft of plumose setae. Uropods normal in form, lateral spine of outer branch strong.

Color in life from a brilliant to a pale salmon red, with the black mandibular spot conspicuous.

DISCUSSION: These specimens show a variation in the form of the chelipeds reminiscent of the species of *Athanas*. Mature males and females have chelae as described above; slightly smaller specimens of both sexes have a large and a small chela (Fig. 1*r*, *s*); small specimens have both chelae similar to the smaller one of the asymmetrical pair. No other marked variation was noted with sex or maturity.

The differences between this species and *M. minutus* are few but conspicuous (contrast Fig. 1 and Fig. 2). The stylocerite of *M. lohena* reaches to the end of the first antennular article, that of *M. minutus* to the middle of the second; the scaphocerite reaches to the end of the antennular peduncle on this species, to the middle of the third article on *M. minutus*. More important are the differences in the chelae, with none of the numerous specimens of *M. minutus* showing the enlarged chelae; and with the fingers in all definitely shorter than the palm, while in *M. lohena* both the large and small type of chela have fingers longer than the palm; also, in *M. minutus* the fingers are quite straight and heavy, while in *M. lohena* the fingers are slender and show at least some curvature. Another possible difference is the degree of coverage of the eyes, with the eyes completely concealed in all specimens of *M. lohena,* and with them usually protruding in some degree from under the carapace in *M. minutus;* however, as the eyes may be rolled forward and backward, this characteristic should not be relied upon. There are no other conspicuous differences in the morphology of the two species. The color in life of the two species, including the black mandibular spot, is the same.

They are also similar in their environments. The habitat of *M. lohena* is described above; while surface layers of the water in the undisturbed pond were almost fresh, the under layers

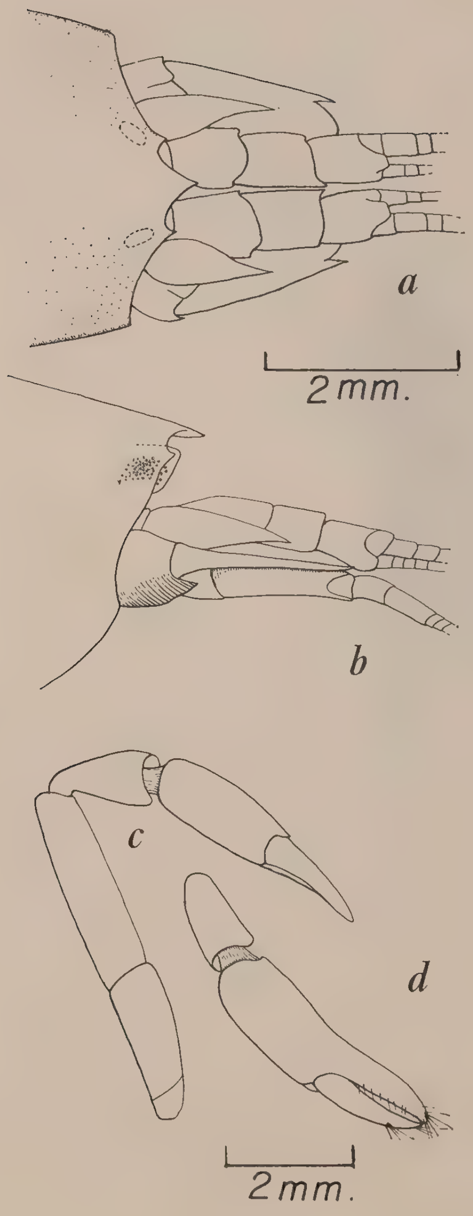

FIG. 2. *Metabetaeus minutus* (Whitelegge). *a, b,* Anterior region, dorsal and lateral aspects; *c,* cheliped; *d,* chela, outer face.

were definitely brackish, and the level of the water in the pool changed with the tides.

M. minutus was collected in two pools on Jaluit. On the islet of Medyado it was found in a mangrove swamp; the base of this swamp was an old reef flat, cut off from both the ocean and the lagoon by boulder and sand ramparts, and through the coral platform flowed definitely brackish water, rising and lowering not only with the tide but also with rapid periodicity of the waves on the ocean reef. The water flowed in and out through a series of ragged holes, and it was in these holes that the shrimp hid, emerging to the surrounding pools when unmolested. On Jabor the shrimp were found in a bomb crater in the center of the islet; the crater was almost dry at low tide and the shrimp were withdrawn into the holes of the coral at the base; but at high tide, when it was almost waist deep with brackish water, the shrimp emerged in great numbers.

However, in the ecology of the pools the two species appear to play entirely different roles. In the pool of Lohena there were two species of shrimp found; the smaller and much more abundant atyid was identified by Rathbun (1906: 919) as *Caridina brevirostris* Stimpson and the larger as *Metabetaeus.* The atyid, abundant in pools of subterranean origin about the Hawaiian Islands, is an herbivore evidently feeding upon the algae growing on the rocks of the pools and upon vegetable detritus falling into the pool. When undisturbed it settles in large numbers on rock surfaces, occasionally walking or swimming from rock to rock. The alpheid, about twice the size of the atyid, usually hides in the rubble at the bottom of the pool, or in cracks in its side, and makes sudden forays to capture the atyid in its long rapacious chelae. It carries the struggling atyid in its chela towards its mouth and disappears again into a hiding place, presumably to eat its prey.

On the other hand, while in the pools of Jaluit there was also an atyid (not as yet identified); the mature atyid and alpheid were of nearly the same size, and the alpheid was by far the more abundant and gave no evidence of predatory habits. Like the *Caridina* in Hawaiian pools, *M. minutus* would emerge to rest on the rocks and vegetable debris in the pool;

they were never seen attacking other shrimp. When the senior author stood bare-legged in the pool while collecting, shrimp settled on his leg and produced a feeling similar to a gentle rasping rather than pinching. In the food groove between the bases of the thoracic legs and among other mouth parts were found sand and detritus. Therefore, they are presumed to be other than carnivorous.

Coutière remarked that in his specimens of *M. minutus* there were spots similar in color to the mandibular spots found about the gill chambers and other parts; he suggested that they were caused by symbiotic zooxanthellae. In none of these specimens of either species were there spots other than the mandibular spots and the normal red chromatophores; moreover, in view of the habit of these shrimp, of living in darkness or semidarkness, it is unlikely that they would have an association with symbiotic algae.

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Reprinted from
AMERICAN JOURNAL OF PHYSIOLOGY, Vol. 199, No. 4, October 1960
Printed in U.S.A.

Effects of corticosteroids on electrolyte metabolism during osmoregulation in teleosts

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Effects of corticosteroids on electrolyte metabolism during osmoregulation in teleosts[1]

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Edelman, Isidore S., Ho Lee Young and John B. Harris. *Effects of corticosteroids on electrolyte metabolism during osmoregulation in teleosts.* Am. J. Physiol. 199(4): 666–670. 1960.—The effects of injections of hydrocortisone, 9 α fluorohydrocortisone and *d,l* aldosterone on rates of loss of Na and K and on serum and muscle electrolyte concentrations were studied in euryhaline and stenohaline marine teleosts during immersion in fresh water for periods of 1–16 hours. Survival time was not affected by administration of adrenal steroids. Survival in fresh water was inversely correlated to the rates of Na loss. Administration of corticosteroids had no consistent effect on either Na or K loss or on the changes in plasma or muscle electrolyte content during immersion in fresh water. It is inferred from the data that euryhalinity depends on the ability to conserve Na, K and Cl in hypotonic water and that NaCl depletion, extracellular fluid contraction and hypovolemia are major factors in the failure of marine teleosts to survive in fresh water.

Evidence to suggest the participation of pituitary, thyroidal and adrenal mechanisms in osmoregulatory responses in fish has been reported by a number of investigators. The pathways of hormonal control of osmoregulation, however, are still undefined (1). Although adrenal cortical hormones have been identified in the blood of teleosts, it has not been shown that their effects on electrolyte transport are similar to those observed in mammals (2–5). Previous studies noted that injection of adrenal cortical extracts and of ACTH failed to promote tolerance to salt water in stenohaline fresh water trout and that neither ACTH nor DCA enabled hypophysectomized Fundulus to survive in fresh water (4, 6). These findings, however, do not definitively exclude steroidal control of electrolyte transport in fish, particularly since they were obtained before the principal mineralocorticoid, aldosterone, was generally available for use. We, therefore, studied the effects of three types of adrenal steroids on electrolyte excretion and on plasma and muscle electrolyte concentrations in euryhaline and stenohaline marine teleosts subjected to immersion in fresh water.

MATERIALS AND METHODS

Nonspawning fish collected from Hawaiian waters were studied during the month of July, 1958. To cover a wide range of adaptive osmoregulatory behavior, three species were studied: stenohaline wrasse (*Thalassoma dupperey*), which is found only in sea water; partially euryhaline marine mullet (*Mugil cephalus*), which inhabits sea water and the brackish waters of the mouths of streams and rivers; and euryhaline tilapia (*Tilapia mossambica*), which adapts readily to sea water, although of fresh water origin (Africa). The body weight of the wrasse averaged 54.6 gm (range 36.5–110.5 gm), of the mullet, 194.0 (range 75.2–382.0 gm) and of the tilapia, 85.7 (range 54.7–142.8 gm).

The tilapia had been collected before the study period and held for weeks to months in large marine ponds. The mullet and wrasse had either been similarly collected and held or were freshly caught. This difference in handling did not appear to affect the results. All fish were kept, without food, in running sea water in large holding tanks for 6–60 hours immediately before study. Each fish was injected intraperitoneally with either distilled water or one of three types of adrenal cortical steroids. It was then placed in sea water for 30 minutes, rinsed in tap water and transferred to a small aerated aquarium which contained only fresh tap water. Wrasse and tilapia were each immersed in 1.5 liters of water and mullet in 4–6 liters. Before the fish was placed in the aquarium the tap water was aerated vigorously for at least an hour to remove all traces of chlorine. The period of incubation in fresh water was 1–3 hours for wrasse, either 7 or 16 hours for mullet and 16 hours for tilapia. Some fish were kept in sea water and not given hormones to serve as controls for the effects of transfer to fresh water.

The hormones were given in the following doses, in 0.25 ml of distilled water: mullet received either 2.5 mg

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Received for publication March 28, 1960.

[1] This study was supported by grants-in-aid from the Public Health Service (H-1441 and A-2676) and the Pauley Fund of the University of California. Contribution No. 134, Hawaii Marine Laboratory.

[2] Advanced Research Fellow of the American Heart Association.

TABLE. 1. *Survival of Marine Fish in Fresh Water*

	IMMERSION TIME (HR.)	HORMONE	NUMBER OF FISH		% SURVIVAL
			TESTED	SURVIVED	
WRASSE	3	NONE FLUOROHYDROCORTISONE ALDOSTERONE	17 4 13	0 0 0	0
MULLET	7	NONE HYDROCORTISONE FLUOROHYDROCORTISONE ALDOSTERONE	6 6 6 6	6 6 6 6	100
MULLET	16	NONE HYDROCORTISONE FLUOROHYDROCORTISONE ALDOSTERONE	10 8 8 8	7 5 8 7	70 63 100 88
TILAPIA	16	NONE ALDOSTERONE	16 8	15 7	94 88

of hydrocortisone succinate (Upjohn), 2.5 mg of fluorohydrocortisone (Merck, Sharp & Dohme) or 5 μg of *d,l* aldosterone monoacetate (Ciba); wrasse and tilapia received 5 μg of aldosterone only. These dosages were calculated to give a maximum effect based on experience in mammals. The fish serving as fresh water controls in each series received intraperitoneal injections of 0.25 ml of distilled water.

Samples of water from the aquaria were collected within 3 minutes after introduction of the fish and at the end of the period of immersion. Blood was obtained from the heart by percutaneous puncture after removal of the fish from the tanks. Because of their small size, we were unable to obtain blood from wrasse. The fish were killed by a sharp blow on the head. Samples of paravertebral muscles were removed by sharp dissection and placed in tared weighing bottles. Samples of serum and muscle were also taken from fish that had been maintained in sea water.

The samples were analyzed for Na and K by flame photometry and for Cl by amperometric titration (7). The samples of muscles were dried, pulverized and extracted as described previously (8). Kidney sections were fixed in Bouin's solution and stained with hematoxylin and eosin for histological study.

Several measurements showed only slight differences in the temperature of the water in the marine ponds, holding tanks and aquaria; the temperature readings ranged from 24° to 28°C. An aliquot of sea water from the holding tanks was found to contain 470 mEq/l. of Na, 10.4 mEq/l. of K and 516 mEq/l. of Cl.

RESULTS

Survival of fish after transfer from sea water to fresh water. The results of direct transfer of fish from sea water to fresh water are summarized in table 1. Cessation of spontaneous motion, especially of the gills, and failure to respond to mechanical stimuli were used as the criteria for death. All the wrasse died after 1–3 hours in fresh water. All the mullet were in good condition at the end of 7 hours. Although 79% of the mullet survived 16 hours in fresh water, several appeared to be *in extremis* by this time. Tilapia proved the most adaptable; 92% survived 16 hours of immersion, and all the survivors were in good condition. The injection of adrenal cortical steroids had no apparent effect on the survival of any of the three groups of fish in fresh water.

Excretion of electrolytes. To avoid post-mortem contributions to the loss of electrolytes into the bath water, the incubation period for the wrasse was terminated while they were still alive. Electrolyte excretion rates were also determined for mullet and tilapia which had survived 16 hours of immersion in fresh water.

Table 2 lists the rates of loss of Na and K expressed in milliequivalents per hour per 100 gm of fish, estimated from the electrolyte content of bath water during and after immersion of the fish in fresh water. The rates of loss of Na and K from mullet immersed for 7 hours and for 16 hours did not differ significantly. Na loss always exceeded K loss significantly. The ratio of the mean Na to K loss in the controls was 6.1:1, 6.3:1 and 9.5:1 in wrasse, mullet and tilapia, respectively. Both the rate of Na loss and of K loss decreased in the order wrasse > mullet > tilapia. The comparative differences in sodium and potassium loss between any two of the groups were statistically significant ($P \pm 0.025$), except for the difference between the losses of sodium by mullet and tilapia ($P \sim 0.2$). The rates of Na and K loss and survival potential showed a striking correspondence; the smaller the rates of loss, the longer the survival in fresh water (see tables 1 and 2). Moreover, the total loss of Na and K per unit of body weight from wrasse in 2.5 hours exceeded the total loss from tilapia in 16 hours. None of the adrenal cortical steroids had an appreciable effect on the rates of loss of either Na or K in any of the three groups of fish.

Serum electrolyte concentrations. Figures 1, 2 and 3 present the concentrations of serum sodium (Na_s), potassium (K_s) and chloride (Cl_s) of mullet and tilapia taken

TABLE. 2. *Rates of Loss of Na and K Into Medium During Immersion in Fresh Water (mEq/Hr/100 Gm of Fish)*

HORMONE	WRASSE		MULLET		TILAPIA	
	Na	K	Na	K	Na	K
CONTROL	0.783 ±0.326 n=11	0.129 ±0.046 n=11	0.146 ±0.043 n=12	0.023 ±0.006 n=11	0.105 ±0.040 n=13	0.011 ±0.003 n=13
HYDROCORTISONE			0.154 ±0.046 n=7	0.027 ±0.010 n=8		
FLUOROHYDRO-CORTISONE			0.149 ±0.066 n=11	0.024 ±0.010 n=13		
ALDOSTERONE	0.967 ±0.360 n=11	0.136 ±0.048 n=11	0.140 ±0.064 n=10	0.024 ±0.010 n=11	0.099 ±0.027 n=6	0.011 ±0.003 n=6

Data are mean values ± standard deviations.

$$\text{S.D.} = \pm\sqrt{\frac{\Sigma(X_i)^2 - \frac{(\Sigma X_i)^2}{n}}{n-1}}$$

X = mean value; X_1 = individual datum; n = number of determinations.

directly from sea water and of similar fish immersed in fresh water for 16 hours. These values show remarkable individual variations, even between fish of the same species under the same conditions. In one of the tilapia, the serum electrolyte concentrations were extraordinarily high (Na_s = 354 mEq/l., Cl_s = 308 mEq/l., K_s = 19 mEq/l.) and, therefore, were not included in the calculation of the mean values or shown in the figures. It is clear, however, that Na_s and Cl_s were significantly decreased in mullet after 16 hours in fresh water.

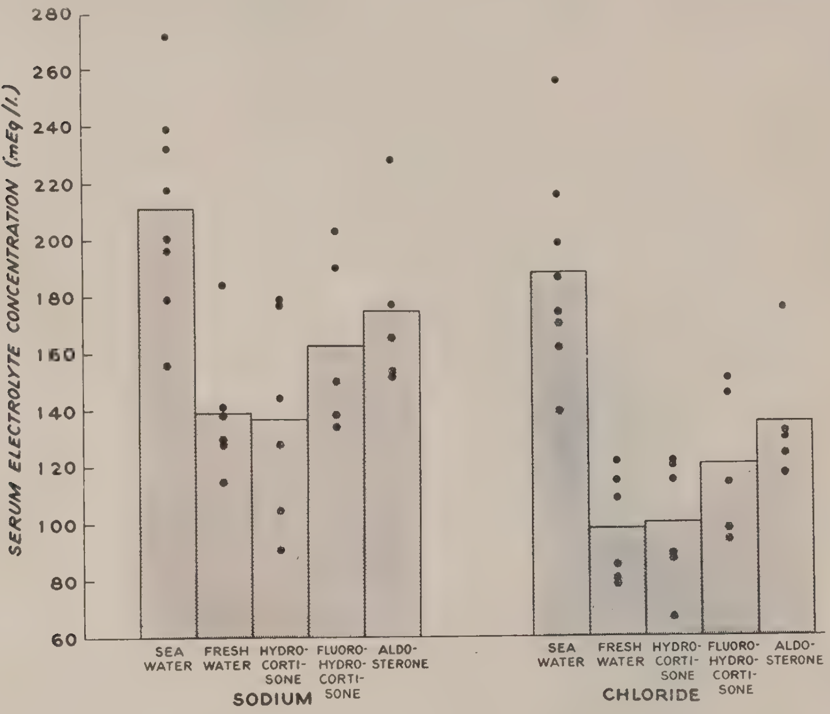

FIG. 1. Serum Na and Cl concentrations in mullet taken directly from sea water compared with concentrations in mullet immersed for 16 hr. in fresh water, without and with injection of adrenal steroids (hydrocortisone succinate, fluorohydrocortisone and *d,l* aldosterone monoacetate). The height of the bar gives the mean value in mEq/l., and each point indicates the individual value.

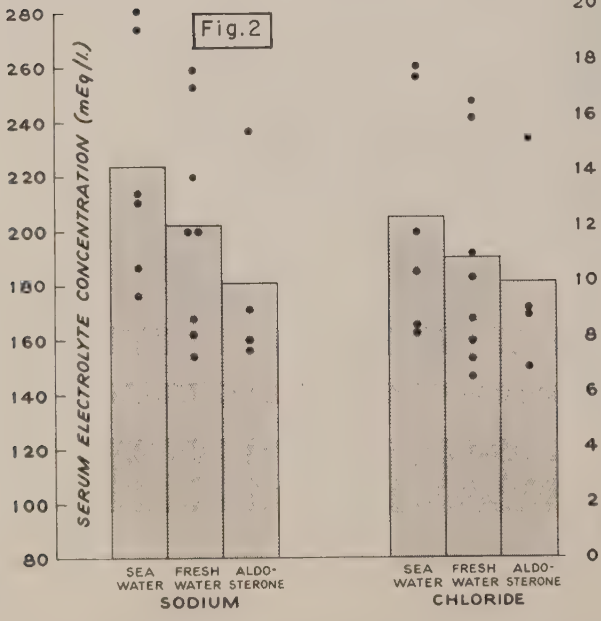

FIG. 2. Serum Na and Cl concentrations of tilapia taken from sea water compared with concentrations in tilapia after 16 hr. immersion in fresh water, without and with injection of *d,l* aldosterone monoacetate. The height of the bar gives the mean value in mEq/l. and each point indicates the individual value.

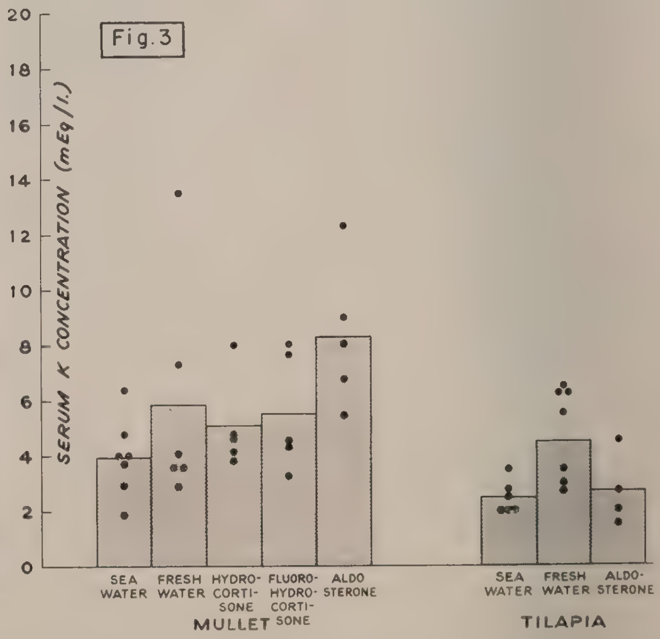

FIG. 3. Serum K concentration of mullet and tilapia taken from sea water or from fresh water, without and with administration of adrenal steroids. The height of the bar gives the mean value in mEq/l. and each point indicates the individual value.

Administration of hydrocortisone had no evident effect on this response, although treatment with 9 α fluorohydrocortisone or aldosterone apparently reduces the magnitude of the decrease. In contrast, only small changes in Na_s and Cl_s were noted in tilapia after 16 hours in fresh water. Administration of aldosterone has little or no effect on this response (fig. 2). These data agree qualitively with the results on the rates of Na loss during immersion in fresh water. As shown in table 2, the rate of sodium loss was about 40% greater in mullet than in tilapia. Interestingly, the Na_s and Cl_s of tilapia and mullet kept in sea water did not differ appreciably, despite the fact that tilapia were originally fresh water fish.

As shown in figure 3, K_s tends to rise after transfer of fish to fresh water, and in a few instances quite high values were recorded. The adrenal steroids had no consistent effect on this response; K_s tended to be higher in the aldosterone-treated mullet and lower in the aldosterone-treated tilapia.

TABLE. 3. *Water Content of Muscle (% Total Wet Weight of Tissue)*

	WRASSE 1-3 HR. IMMERSION	MULLET 7 HR IMMERSION	MULLET 16 HR IMMERSION
SEA WATER		77.5 ±0.5 n = 8	
FRESH WATER	80.9 ± 1.3 n = 11	79.3 ± 1.5 n = 6	80.9 ±0.7 n = 5
HYDROCORTISONE		80.0 ± 1.3 n = 6	81.8 ± 1.3 n = 4
FLUOROHYDRO-CORTISONE		78.9 ± 1.0 n = 6	80.6 ±0.9 n = 6
ALDOSTERONE	80.9 ± 1.1 n = 11	79.4 ±0.8 n = 6	80.3 ±0.5 n = 4

Data as in table 2.

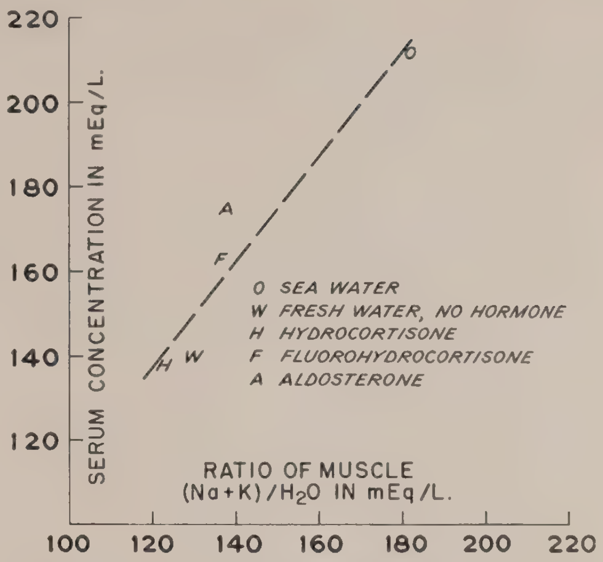

FIG. 4. Mean serum Na concentration in mEq/l. is graphed as a function of the mean ratio of (Na + K) to H_2O content in muscle. The regression line is approximate only. These values were calculated from the data on mullet which are summarized in tables 3 and 4 and fig. 1.

Water and electrolyte content of skeletal muscle. Tables 3 and 4 summarize the water and the Na, K, and Cl content of skeletal muscle taken from fish transferred to fresh water, some of which had been injected with hormones, and from fish kept in sea water. The water content of muscle from mullet in sea water was similar to that of muscle of terrestrial vertebrates (9). A small but definite increase in muscle water content occurred in

TABLE 4. *Electrolyte Content of Muscle (mEq/gm of Tissue, Dry Weight)*

	WRASSE 1-3 HR. IMMERSION			MULLET 7 HR IMMERSION			MULLET 16 HR IMMERSION			TILAPIA 16 HR IMMERSION		
	K	Na	Cl	K	Na	Cl	K	Na	Cl	K	Na	Cl
SEA WATER	0.664 ±0.025	0.088 ±0.011	0.081 ±0.019	0.574 ±0.029	0.049 ±0.021	0.047 ±0.018	0.574 ±0.029	0.049 ±0.021	0.047 ±0.018	0.710 ±0.029	0.085 ±0.026	0.058
	n = 4			n = 8			n = 8			n = 4		n = 2
FRESH WATER	0.626 ±0.038	0.068 ±0.020	0.051 ±0.013	0.542 ±0.013	0.034 ±0.003	0.027 ±0.004	0.519 ±0.041	0.030 ±0.007	0.025 ±0.004	0.632 ±0.059	0.063 ±0.043	0.053 ±0.014
	n = 13			n = 6			n = 6			n = 6		
HYDROCORTISONE				0.543 ±0.020	0.034 ±0.005	0.026 ±0.002	0.522 ±0.045	0.029 ±0.007	0.025 ±0.002			
				n = 6			n = 5					
FLUOROHYDRO-CORTISONE				0.561 ±0.039	0.031 ±0.004	0.030 ±0.007	0.538 ±0.026	0.033 ±0.006	0.026 ±0.006			
				n = 6			n = 8					
ALDOSTERONE	0.622 ±0.026	0.072 ±0.020	0.058 ±0.018	0.535 ±0.044	0.032 ±0.003	0.028 ±0.008	0.531 ±0.042	0.030 ±0.006	0.027 ±0.005	0.644 ±0.046	0.062 ±0.014	0.049 ±0.007
	n = 13			n = 6			n = 7			n = 7		

Data as in table 2.

fish after 7 hours of immersion in fresh water, and an additional small gain was found in fish immersed for 16 hours. None of the adrenal steroids altered this response. Similarly, aldosterone did not alter the water content of muscle in wrasse subjected to 1–3 hours of immersion in fresh water (see table 3).

Table 4 summarizes the data on the electrolyte content of muscle expressed as milliequivalents per gram of tissue (dry weight). The values in fish taken from sea water are similar to those found in terrestrial vertebrates, except that fish muscle appears to be richer in potassium (9). This finding is consistent with the observation that the extracellular osmolality of marine fish is higher than that of terrestrial vertebrates (9).

The consistent decrease in muscle K, Na and Cl content in all three groups presumably reflects the loss of these ions to the fresh water. The fractional decrease in muscle Na and Cl was uniformly greater than the fractional decrease in muscle K. These results agree with the findings on the relative rates of loss of Na and K summarized in table 2. The administration of hydrocortisone or fluorohydrocortisone or aldosterone to mullet or of aldosterone to wrasse and to tilapia did not modify appreciably the changes in the electrolyte content of muscle induced by transfer from sea water to fresh water.

DISCUSSION

The results summarized in tables 2 and 4 indicate that the rate of loss of Na is 6–10 times greater than the rate of loss of K when euryhaline and stenohaline marine fish are transferred directly from sea water to fresh water. The inverse relationship between survival and rates of electrolyte loss of fish after transfer to fresh water supports the contention that euryhalinity is primarily a function of the ability to conserve electrolytes in a hypoosmotic environment (4). The preferential loss of Na from fish subjected to immersion in fresh water is also shown indirectly by the marked declines in the Na content of serum and of muscle (see tables 2 and 4 and figs. 1 and 2). The K content of muscle declined significantly, but K_s was either unchanged or tended to rise after incubation in fresh water. It appears reasonable, therefore, to propose that NaCl depletion, extracellular fluid contraction and hypovolemia are important factors in the stenohalinity of marine teleosts. It is noteworthy that tilapia, a nonmigratory fish of fresh water origin, adapts to undiluted sea water and does not lose its euryhalinity, even after several generations in sea water. Histological examination showed no striking differences in renal tissue from wrasse, mullet and tilapia. All three species have similar glomerular and tubular structures.

Recent studies on mammalian tissues *in vitro* and on changes in Na_s *in vivo* indicate the passive distribution of water across cell membranes in proportion to solute activity (10, 11). Comparable studies during the transient states of osmoregulation in fish have not yet appeared. The data in tables 3 and 4 and figure 1, however, permit an approximate analysis of the osmolarity of plasma and muscle by comparing Na_s to the ratio of total muscle (Na + K) to muscle H_2O (11). Figure 4 shows that in mullet taken from sea water or immersed for 16 hours in fresh water with and without corticosteroids, Na_s and $(Na + K)/H_2O$ correlate approximately linearly. Inasmuch as plasma and cellular osmolarities are given only roughly by Na_s and $(Na + K)/H_2O$, respectively, this finding may be taken as being consistent with, but not proof of, osmotic equilibrium across cell membranes during osmoregulation in fish.

The failure of injected adrenal steroids, including the potent mineralocorticoids, 9 α fluorohydrocortisone and aldosterone, to alter the response of euryhaline and stenohaline marine species to immersion in fresh water may mean that the interrenal gland does not regulate rates of electrolyte transport across the gills or renal tubules in teleosts. The demonstration of appreciable quantities of cortisone, hydrocortisone, corticosterone and aldosterone in the plasma of fish, especially during spawning migration, however, would indicate that the interrenal glands of teleosts synthesize these steroids (2, 3, 5, 12, 13). Furthermore, the data of Fontaine (12) suggest that the activity of the interrenal gland is inhibited by high environmental salinities and stimulated by low salinities. Nevertheless, additional studies are needed to define clearly what role, if any, the adrenal steroids play in osmoregulation in teleosts.

We are grateful for the support and advice given to us by Professor A. H. Banner and the staff of the Hawaii Marine Laboratory. Valuable technical assistance was provided by Mrs. Florence Hook and Mrs. Ruth Carley.

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Hawaiian Lava-Flow Fishes, Part IV

Snyderidia canina Gilbert, with Notes on the Osteology of Ophidioid Families

WILLIAM A. GOSLINE

Reprinted from PACIFIC SCIENCE
October, 1960

Reprinted from PACIFIC SCIENCE, *vol. XIV, no. 4, October, 1960*

Hawaiian Lava-Flow Fishes, Part IV
Snyderidia canina Gilbert, with Notes on the Osteology of Ophidioid Families[1]

WILLIAM A. GOSLINE[2]

ALTHOUGH THE GENUS *Snyderidia* is well marked and well described, it has been assigned at one time or another to four different families. In the attempt to determine the proper family allocation of this genus, it has been necessary to reinvestigate the nature of the families of the suborder Ophidioidea to which it belongs.

The history of *Snyderidia* is as follows. The genus and species (*Snyderidia canina*) were described by Gilbert (1905: 654, 655) from a single specimen 309 mm. in length taken off Kauai of the Hawaiian Islands at a depth of 385–500 fathoms. Another specimen 122 mm. in length was taken by Gosline, Hayes, and Keen from among the fishes killed by the lava flow off Hawaii on June 6, 1950.[3] Gilbert's original description is excellent and applies well to the lava flow specimen. Indeed there is nothing worth adding, so far as external features are concerned. Parr (1933: 49), because of the squamation in *Brotulotaenia*, has suggested that small, embedded scales might be present in *Snyderidia*, but Gilbert is correct in stating that scales in the latter genus are absent.

Snyderidia was placed by Gilbert in the Lycodapidae, a family hitherto represented by the single genus *Lycodapus* from the west coast of North America. However, Regan places *Lycodapus* in the blennioid family Zoarcidae (1912: 276) with the statement:

> *Lycodapus*, Gilbert, includes small deep-sea fishes of the North Pacific, and has been made the type of a distinct family and placed near the Fierasferidae [Carapidae]. But the head and mouth recall those of *Lycodopsis* or *Bothrocara*, the gill-membranes join the isthmus between the rami of the lower jaw (at least in *L. fierasfer*), and the dorsal and anal rays correspond in number to the myotomes.

C. L. Hubbs (*in litt.*) concurs with Regan's placement of *Lycodapus* in the Zoarcidae. On the basis of these allocations I will assume that *Lycodapus* is a blennioid fish and dismiss it from further consideration. Inasmuch as the several dorsal and anal rays per vertebra indicate immediately that *Snyderidia* is not a blennioid, it cannot be placed in the same family with *Lycodapus*.

Smith and Radcliffe (in Radcliffe, 1913: 175) described *Pyramodon*, a genus very similar in appearance to *Snyderidia*, and placed both genera in the Carapidae.

However, Regan (1914: 20) included these genera in the Brotulidae with the following explanation:

> In many respects these two genera seem to connect the Brotulidae with the Fierasferidae, but I have ascertained that *Pyramodon* agrees with the Brotulidae in the structure of the upper surface of the skull, the supraoccipital separating the rather small parietals.

Smith (1955: 546) tentatively assigns *Snyderidia* to his family Pyramodontidae, which is distinguished as follows:

I. Parietals small, separated by supraoccipital. Maxilla well expanded posteriorly. Usually pyloric caeca. Pelvics usually present. Pectorals normally with more than 20 rays.
    A. Dorsal origin well in advance of anal origin and vent, the latter behind pectoral origin. Scales usually present. Dentition feeble. Spines on opercular bones usually present. Preopercle margin usually free..........................Brotulidae

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[1] Contribution No. 135, Hawaii Marine Laboratory. Previous papers on these same collections of fishes were: I, The Origin and Nature of the Collections; II, Brotulidae; and III, Sternoptychidae. All of these previous sections were published in this journal.

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[3] A third specimen of this species is mentioned by Radcliffe (1913: 176), but he does not state where it was taken. Schultz and Kanazawa (*in litt.*) provide the information that this third specimen is USNM 99230, collected in the Philippines.

B. Dorsal origin opposite anal origin and vent, all far forward, at level of or not far behind pectoral origin. No scales. Dentition powerful, large canines. No opercular armature. Hind preopercle margin entirely below skin..........Pyramodontidae

II. Parietals moderate, meet on midline. Maxilla not or barely expanded posteriorly. Pelvics absent. Scales absent. Vent and anal origin usually anterior to dorsal origin. Pectorals with less than 20 rays......Carapidae

Arnold's (1956) revision of the Carapidae contains no mention of either *Snyderidia* or *Pyramodon.*

In sum then, *Snyderidia* has been placed in the Lycodapidae, Carapidae, Brotulidae, and tentatively in the Pyramodontidae. As the first of these allocations is almost certainly erroneous, the problem that remains is to determine the relationship of *Snyderidia* to other ophidioid groups.

Aside from Smith's recent erection of the Pyramodontidae and the synonymizing of the Disparichthyidae with the Carapidae (see de Beaufort, 1951: 449; Arnold, 1956: 260, 261), the classification of the ophidioid fishes stems directly from Regan (1912). Three ophidioid families, distinguished by the characters listed in Table 1, were there recognized. So far as can be determined from Regan's paper, the internal features recorded are based on skeletons of a single species from each family: *"Brotula jayakari"* of the Brotulidae, *"Genypterus blacodes"* of the Ophidiidae, and *"Fierasfer acus"* of the Carapidae.

If these were small and uniform families one might allocate *Snyderidia* by simple reference to Table 1. However, the possibility of both internal and external diversity exists in all three and has been abundantly verified in the Brotulidae (cf. Norman, 1939: 83, 84; Gosline, 1953: 220–225). In view of this, it seems advisable to use a much broader base than Regan's for the establishment of family definitions among the ophidioid fishes. Unfortunately such a base is only partly available.

So far as the external features generally used are concerned, some members of the tremendous family Brotulidae nearly overlap the Ophidiidae, whereas others grade almost imperceptibly by way of Smith's Pyramodontidae into the Carapidae. Whether external characters exist in these families that would provide better definitions remains unknown to this author, for only a few forms are available for examination.

The present paper therefore will be concerned primarily with osteological features. Skeletons that have been used here are those of *Microbrotula, Dinematichthys,* and *Brotula* previously prepared (Gosline, 1953), of *Snyderidia,* and of a specimen of (presumably) *Otophidium*[4] (without data) received from the U. S. National Museum. The following literature on internal features has also been referred to: Emery (1880), Regan (1912), and Arnold (1956).

Cranium: Unlike the other crania at hand, that of *Snyderidia* is thin walled and rather fragile. The sutures in many instances—e.g., on the back of the skull, between the lower portion of the sphenotic and pterotic, and in the alisphenoid area—are difficult to make out, and in Fig. 1*a* and *b* some of these have been drawn with considerable misgiving.

Regan (1912) made use of three cranial characters in separating the Brotulidae from the Carapidae (Table 1, nos. 6–8). Two of these concern the development of the supraoccipital. According to Regan (1912) the parietals are

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[4] In view of the varied interpretations of ophidiid genera (cf. Harry, 1951; Norman, ms., 1957) it seems advisable to give a brief description of the specimen skeletonized.

Total length 185 mm. Pelvics inserted about below the anterior border of the pupil, the outer filaments a little over twice as long as the inner. Gill membranes attached to the isthmus below rear border of eye. Four developed gill rakers. Pseudobranch consisting of about five short filaments. Head scaleless. No spine on snout tip. Opercle ending in a strong, concealed, little flattened spine. Anterior nostril on snout rim; posterior about midway between snout rim and anterior border of eye. Teeth many-rowed on jaws, vomer, and palatines, the rows tapering in width from front to rear. Outer jaw teeth rather long, curved, and sharply conical; inner similar but smaller, straighter, and blunter. Preorbital not differing greatly from suborbitals.

Scales on body rectangular, not embedded and not overlapping, the long axes of adjacent scales frequently at right angles to one another. Dorsal and anal rays covered with flesh, dark edged posteriorly and around tail. Air bladder short, terminating rather abruptly posteriorly, with a hole in its posteroventral face.

TABLE 1

DIFFERENCES BETWEEN OPHIDIOID FAMILIES NOTED BY REGAN (1912: 277–280)

BROTULIDAE	OPHIDIIDAE	CARAPIDAE
1. Pelvic fins, when present, jugular	Pelvic fins inserted between rami of lower jaw	Pelvics absent
2. Vent remote from head		Vent placed at throat
3. Gill openings wide, with gill membranes separate and free from isthmus (except in *Dermatopsis*)	Gill membranes attached to isthmus behind pelvics	
4. Mouth protractile		Mouth nonprotractile
5. Pterygoid and mesopterygoid separate	Pterygoid and mesopterygoid ankylosed	
6. Parietals separated by supraoccipital		Parietals meet above supraoccipital
7. Supraoccipital forms, with exoccipitals, a strong median crest which does not project above upper surface of skull		Occipital crest is weak, and exoccipitals do not take part in its formation
8. Opisthotic is not enlarged, though basioccipital and prootic form a rather prominent auditory bulla		Enlarged opisthotic reaches basioccipital, sharing with that bone and prootic in formation of auditory bulla
9. Lower fork of posttemporal is directly attached to opisthotic	Lower fork of posttemporal is shortened and attached to opisthotic by ligament	Lower fork of posttemporal is reduced to a little knob
10. Coracoid and scapula are separated by cartilage	Coracoid and scapula are in contact	Coracoid and scapula are in contact
11. Cleithra normal	Cleithra prolonged within isthmus as a pair of slender processes, with pelvic bones attached to their extremities	
12. Vertebrae (in *Brotula multibarbata*) 15 + 40	Vertebrae (in *Genypterus blacodes*) 20 + 52	Vertebrae (in *Carapus acus, fide* Emery) 125–144, of which 17 or 18 are precaudal; 26 precaudal vertebrae in *Carapus dentatus*
13. First 5 vertebrae with sessile ribs, 3rd and 4th pairs being expanded	First 5 vertebrae with sessile ribs, but only 3rd expanded	
14. Strong transverse processes on vertebrae 6–15	Parapophyses on vertebrae 6–11 are strong and broad, much as in *Merluccius;* rest are normal	

separated by the supraoccipital in the brotulids but meet above in the carapids. I have already shown (1953: 232) that *Dinematichthys*, among three brotulids examined, had the parietals meeting above. In *Otophidium* as well as in "*Ophidium Rochei*" (Emery, 1880, pl. 3, fig. 26) the parietals are separated by the supraoccipital. In *Pyramodon* (acc. Regan, 1914) they are separated, but in *Snyderidia* and the two carapids figured by Emery (1880, pl. 3, figs. 18, 23) they meet. Whether the parietals are separated or meet is correlated with the size of the occipital crest (Table 1, no. 7); among the skeletons available it would seem that the supraoccipital is best developed in the narrow, highheaded forms, e.g., *Otophidium* (Fig. 1*c*), and least developed in the broad, flatheaded species, e.g., *Dinematichthys*. That the size and extent of the supraoccipital have any great systematic value in this suborder seems questionable.

The relative size of the opisthotic (Table 1, no. 8) is another feature variable within the brotulids (Gosline, 1953, table 3). The opisthotic of *Otophidium* (Fig. 1*c*) and *Snyderidia* (Fig. 1*b*) is expanded.

Three other cranial features of *Otophidium* and *Snyderidia* seem worth noting. In *Otophidium* the exoccipital facet for the articulation of the first vertebra forms a single concave wall of nearly uniform depth; in the available brotulids and in *Snyderidia* this articulation is formed by the usual two projecting pads. In *Snyderidia* I can find no trace of a suture between the frontals (Fig. 1*a*). Finally, in the same genus, as frequently in carapids, there is a greatly enlarged canine tooth at the front of the vomer (Fig. 1*b*).

Suspensorium: Regan (1912) has used the fusion vs. nonfusion of the ectopterygoid and mesopterygoid as a distinction between the Ophidiidae and the Brotulidae. In the three brotulid skeletons available the mesopterygoid and ectopterygoid are indeed joined by suture, whereas in the ophidiid they are fused. Emery (1880, pl. 3) shows the mesopterygoid and ectopterygoid of two species of carapids as suturally joined. In *Snyderidia* (Fig. 2) I have been able to find no trace of a suture between the ecto- and the mesopterygoid, but, as already noted, I have had difficulty locating the sutures between several of the other head bones in this specimen.

Another variable character in the ophidioid fishes is the position and size of the metapterygoid. In *Brotula* this bone completely separates the hyomandibula and mesopterygoid. In the other two brotulid skeletons, as in *Otophidium*, the latter two bones barely meet in front of the metapterygoid, and in *Snyderidia* (Fig. 2) there is a broad mesopterygoid-hyomandibula junction in front of the metapterygoid.

In *Snyderidia* (Fig. 2), as in *Otophidium*, the hyomandibular strut that runs back across the inner face of the preopercle to form the articulation with the opercle is long and narrow, not short and strong as in *Brotula*.

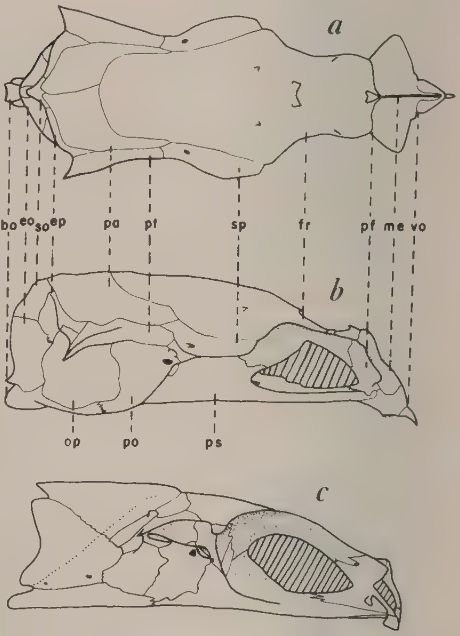

FIG. 1. Skulls of: *Snyderidia*, *a*, top view, *b*, side view; *c*, of *Otophidium*, side view. The dotted line in *c* represents the approximate limit of the occipital crest. *bo*, Basioccipital; *eo*, exoccipital; *ep*, epiotic; *fr*, frontals; *me*, mesethmoid; *op*, opisthotic; *pa*, parietal; *pf*, prefrontal; *po*, prootic; *ps*, parasphenoid; *pt*, pterotic; *so*, supraoccipital; *sp*, sphenotic; *vo*, vomer.

Opercular bones: The opercle in *Snyderidia* is formed of two struts extending out like the wings of a V from the opercle-hyomandibular articulation. The upper of these wings ends in a point; the lower is broadly rounded distally. The structure is not very different from that in *Otophidium* or the illustrations of carapids given by Emery (1880, pl. 3).

Jaws: Except for the large canine tooth at the front of the premaxillary of *Snyderidia*, I am unable to find significant differences between it, *Otophidium*, and the three brotulid genera. The upper jaw of *Snyderidia* is about as drawn by Emery (1880, pl. 3, fig. 25) for *"Fierasfer dentatus."*

The lower jaw in carapids has been dealt with recently by Arnold (1956) who distinguishes three types within the family. The mandible of *Snyderidia* (Fig. 2) very definitely falls with type B of Arnold (1956, fig. 3; see also Emery, 1880, pl. 3, fig. 25). The lower double rim of this jaw type is also found in *Otophidium* but not in the available brotulid skeletons.

A curious feature of the lower jaw of *Snyderidia* is that in dissection the angular on both sides, together with its ligamentous attachment

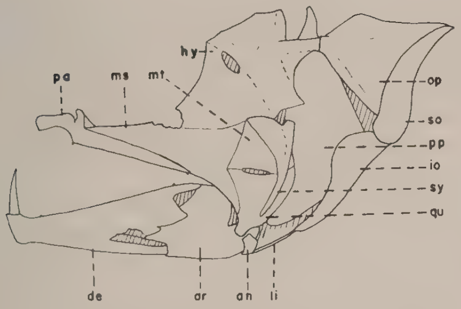

FIG. 2. Right suspensorium, mandible, and opercular bones of *Snyderidia*, from inside. Interosseous areas hatched. *an*, Angular; *ar*, articular; *de*, dentary; *hy*, hyomandibular; *io*, interopercle; *li*, ligament between angular and interopercle; *ms*, mesopterygoid and ectopterygoid; *mt*, metapterygoid; *op*, opercle; *pa*, palatine; *pp*, preopercle; *qu*, quadrate; *so*, subopercle; *sy*, symplectic.

to the interopercle (Fig. 2), came free from the rest of the jaw. Presumably it was loosely connected by ligament with the articular, rather than united with it by suture as in the other ophidioids available.

Visceral arches: The hyoid apparatus of *Snyderidia* seems to show no unusual features. There are seven branchiostegal rays: five on the ceratohyal and two on the epihyal. The urohyal is short and has the configuration of an inverted T.

The first gill arch in *Snyderidia* contains two rows of spinous patches. The outer row below contains about 13 spinous patches in front plus three elongate struts; the uppermost of these is at the angle. Each of these struts, i.e., developed gill rakers, has a whole series of spinelets projecting from its inner surface. On the upper portion of the gill arch (above the angle) there are 3 patches of spinelets in the outer row.

The basibranchial area between the bases of the 2nd gill arch and the pharyngeals consists of an elongate raised ridge with teeth. There are basibranchial teeth in some brotulids (cf. Gosline, 1954: 77, fig. 3), but none are present in those for which skeletons are available. The basibranchials of *Otophidium* are also toothless, but Emery (1880, pl. 5) shows basibranchial teeth in *"Fierasfer acus."*

In *Snyderidia* there are the usual pair of separate toothed lower pharyngeals and three pairs of toothed upper pharyngeals.

Regan has used the gill membranes as a character for separating most of the brotulids from the carapids (Table 1, no. 3). In *Snyderidia* Gilbert (1905: 654) states: "Gill-openings continued forward to below eye; gill membranes separate, free from isthmus." In this feature, and *Pyramodon* is similar, *Snyderidia* belongs with the brotulids.

Pectoral girdle and fin: The bones of the primary pectoral girdle are very light and difficult to make out. Apparently they are similar to those drawn for *"Fierasfer"* by Emery (1880, pl. 4, fig. 35). The coracoid and scapula are in contact, and there is a small scapular foramen.

Regan differentiates the Brotulidae from the other two ophidioid families in having the coracoid and scapula separated by cartilage. This is certainly true of *Brotula*. However, in *Dinematichthys* the scapula and coracoid seem to be nearly in contact (Fig. 3*b*). Be that as it may, the primary pectoral girdle is so poorly developed in all the ophidioid skeletons available that it would seem inadvisable to attach much importance to differences between them.

In the secondary pectoral girdle, Regan has used the structure of the posttemporal as a character for distinguishing families (Table 1, no. 9). However, the distinctiveness of the posttemporal structure as stated by Regan is greater than in the fishes. Whether the lower posttemporal limb articulates directly or by ligament with the opisthotic is difficult to determine in available skeletons; in all, the tip of the lower limb of the posttemporal closely approaches the opisthotic, but even in *Brotula* the main attachment between the two bones appears to be ligamentous.

There is indeed considerable differentiation among the relative sizes of the two posttemporal wings in the skeletons at hand. In *Brotula* both prongs are about equally long; in *Otophidium* the upper prong is nearly five times as long as the lower (Fig. 3*a*); the other brotulids and *Snyderidia* fall between *Brotula* and *Otophidium* in the relative lengths of the posttemporal wings.

Vertebral column: The vertebral column has perhaps been used more than any other internal structure in differentiating groups of ophidioid fishes. In addition to the features noted by Regan (Table 1, nos. 11–14), various authors have noted the peculiar first vertebra of the Ophidiidae, and Arnold (1956) has recently discussed several aspects of the vertebral column in the carapids.

Posteriorly, the vertebral column of carapids and *Snyderidia* tapers to nothing, and there is no hypural fan (Emery, 1880, pl. 2). In brotulids, the caudal skeleton is quite variable, some species having a moderately well-developed hypural structure (Gosline, 1953, fig. 2b, which unfortunately is upside down); in others (Gosline, 1953, fig. 2a, c) no hypural fan whatever seems present. In *Otophidium* the caudal skeleton is about as in *Dinematichthys* (cf. Gosline, 1953, fig. 2b), i.e., moderately well developed.

At the anterior end the first vertebra shows considerable variation in the different ophidioids. For example, among the skeletons examined *Otophidium* has a rather more specialized method of articulation between the skull and the vertebral column than the others, and the neural arch of the first vertebra is heavy, with the two sides fused above, but low and rounded (Fig. 4*a*). In *Snyderidia* the two sides of the first neural arch extend up and back but are short and barely meet above. In the three brotulids (see Fig. 4*b*) the first neural arch has about the same inclination but is higher and is closely appressed against the second. In the carapids according to Emery (1880, pl. 5) and Arnold (1956) the first neural arch projects upward and forward.

One or more of the first few pairs of ribs in *Brotula*, *Otophidium* (cf. Müller, 1843; Facciola, 1933), and *Carapus* (cf. Emery, 1880) is closely associated with the air bladder. The nature of these first ribs has been used by Regan (Table 1, no. 13) to differentiate ophidioid families. In *Brotula* (Fig. 4*b*) and *Dinematichthys* the ribs on vertebrae one and two are sessile and unexpanded; in *Snyderidia* the first two ribs are sessile but somewhat expanded; in *Otophidium* the first vertebra and its ribs (Fig. 4*a*) are exceedingly specialized. In *Brotula* and *Dinematichthys* the ribs on the third and fourth vertebrae are separate, sessile and more or less expanded. In *Snyderidia* the rib on the third vertebra is sessile and considerably expanded but that of the fourth is minute and attached to a long parapophysis. In *Otophidium* the second vertebra seems to lack ribs; the third, fourth, and fifth have sessile ribs, of which that from the third runs medially to the air bladder.

As to the number of transverse processes (Table 1, no. 14), there is in *Otophidium*, at least, the probability that "transverse processes" and "sessile ribs" are actually the same structures, the distinction being merely one of definition, i.e., it would appear that in this fish a "transverse process" that has a basal articulation with the centrum becomes a "sessile rib" (cf. Emery, 1880, pl. 5, fig. 50, c_4). Nevertheless the old

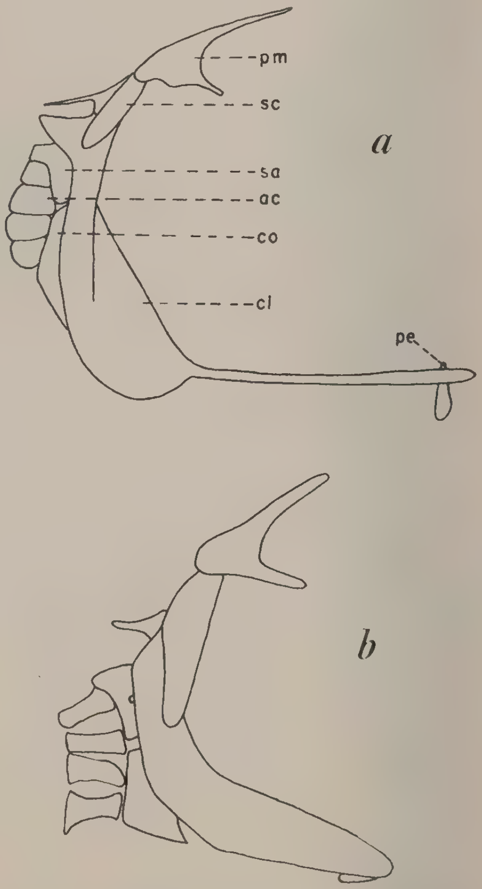

FIG. 3. Right pectoral girdles of, *a*, *Otophidium* and, *b*, *Dinematichthys*, from outside. *ac*, Actinost; *cl*, cleithrum; *co*, coracoid; *pe*, pelvic girdle; *pm*, posttemporal; *sa*, scapula; *sc*, supracleithrum.

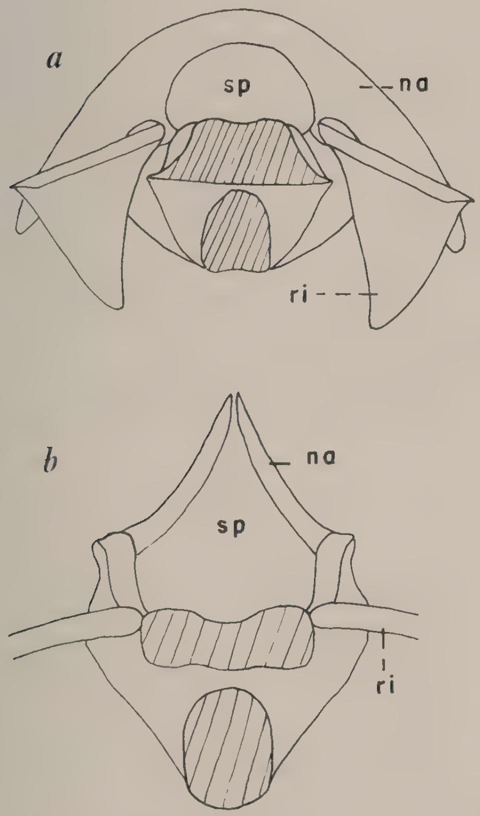

FIG. 4. First vertebra and ribs of, *a, Otophidium* and, *b, Brotula,* from front. Surfaces for articulation with skull hatched. *na,* Neutral arch; *ri,* rib; *sp,* space containing spinal cord.

terminology will be used in order to deal with character no. 13 of Table I. In *Brotula* the first five vertebrae have "sessile ribs"; in *Dinematichthys* the first six; in *Otophidium* the first, third, fourth, and fifth; and in *Snyderidia* the first three only. (In *Microbrotula* ribs are now lacking from several of the front vertebrae, but they may well have been lost in the process of skeletonization.) Judging from Emery's plate (1880, pl. 5) sessile ribs are present on the first four vertebrae of *"Fierasfer acus"* and *"Fierasfer dentatus";* in the latter species each rib is separate, but in the former the ribs of vertebrae three and four have apparently fused into a single plate (see also Arnold, 1956, fig. 2c). According to Arnold (1956: 257, fig. 5) a third group of carapids has the transverse processes ("sessile ribs") of vertebrae three, four, and five fused into a single plate.

Regan has also used the number of "strong transverse processes" as a character for separating the brotulids from the ophidiids (Table 1, no. 14), but this is certainly a variable character in the brotulids. For example, *Microbrotula* has transverse processes only on vertebrae eight through eleven, whereas *Hypopleuron* (see Radcliffe, 1913, pl. 14) has greatly expanded parapophyses on vertebrae four to fourteen (which partly enclose the air bladder).

A final vertebral character is the number of abdominal and caudal vertebrae (Table 1, no. 12). In the three brotulids skeletonized counts are: *Brotula,* 15 abdominal + 46 caudal; *Microbrotula,* 12 + 40; *Dinematichthys,* 12 + 34; in *Otophidium,* 16 + 53; in *Snyderidia,* 15 + 58. Emery (1880: 26) gives 125–144 vertebrae for *"Fierasfer acus,"* of which 17 or 18 are abdominal. Arnold (1956) uses the number of trunk vertebrae as one basis for dividing the carapids into three sections, one group having 17–20, another 27 or 28, and a third 30 or 31.

Internal soft anatomy: The air bladder of *Snyderidia* is apparently simple and extends from below the second to below the twelfth vertebra. According to Gilbert (1905: 654) *Snyderidia* has two pyloric caeca.

External characters: Only a few of the external features of *Snyderidia* need be noted. First, the species resembles the carapids in the presence of a long tail that tapers gradually to nothing. Second, though the pectoral of the lava flow specimen of *Snyderidia* has been rather badly frayed, it is possible to count 27 rays on one side. This high count seems to place *Snyderidia* with the brotulids and ophidiids rather than with the carapids (Smith, 1955: 546). Finally, there are no scales whatever.

Relationships: On the basis of the foregoing comparison *Snyderidia* would appear well differentiated from the Ophidiidae, Brotulidae, and Carapidae, but is probably closest to the last. Especially notable carapid characteristics in *Snyderidia* are the absence of pelvic fins, the long anal fin, the tapering body, the lack of scales, and perhaps especially the dentition. Indeed, in all these respects and notably in lower jaw structure *Snyderidia* bears a considerable resemblance to the carapid genus *Echiodon* (Arnold, 1956). Nevertheless, in another whole series of characteristics *Snyderidia* differs from *Echiodon* and apparently all other carapids. This series may be divided between presumably primitive and presumably specialized features. Among the "primitive" characters in *Snyderidia* may be mentioned the wide gill openings; the comparatively low number of vertebrae, both abdominal and caudal; the relatively high pectoral count; the small, backwardly sloping first neural arch; and the protractile upper jaw. In all these traits *Snyderidia* is closer to the brotulids and ophidiids than to the carapids. Among specialized features in *Snyderidia* may be mentioned especially the fusion of the frontals and the separate angular bone. On the whole then *Snyderidia* might be considered a side branch of the primitive stock from which the carapids have arisen. In the absence of known transitional forms between *Snyderidia* and the carapids, *Snyderidia* would appear to merit separation at the family level.

Though the internal features of *Pyramodon* remain mostly unknown, it seems most probable that *Snyderidia* should be included in Smith's family Pyramodontidae. The chief external difference between the two appears to be the retention of pelvic filaments in *Pyramodon.* To include *Snyderidia,* some slight rearrangement of Smith's definition (see above) of the family seems required. Using only those characters known for both *Pyramodon* and *Snyderidia,* the family Pyramodontidae may be redefined as follows: Body naked, tapering to a fine point posteriorly. Anal fin commencing below the pectoral. Pectoral with 27 rays. Gill openings extending well forward on throat. Upper jaw protractile. Large canines on the front of the vomer and at the symphyses of both jaws.

Some discussion of the remaining ophidioid families seems in order. The Carapidae is obviously the most specialized; indeed in habits the Carapidae is among the most specialized of all fish families, for it and the unrelated Pygidiidae comprise the only two fish families known that have developed parasitic members.

The Ophidiidae is externally separable from the other families in the group by the mental pelvics, though certain brotulid genera have the pelvics nearly as far forward. A more important character, if it applies to all ophidiids, is the peculiar first neural arch (Fig. 4*a*) and its connection with the air bladder; unfortunately this feature remains uninvestigated in what Norman (ms., 1957: 500) calls the subfamily Lepophidiinae.

The Brotulidae is a tremendous and heterogeneous family (Gosline, 1953), which Norman has recently divided into four subfamilies (ms., 1957: 484). That its osteological features cannot be characterized on the basis of internal examination of one species has been abundantly shown, while even the approximate limits of variation remain unknown. Suffice it to say that even the known variation in osteological features (Gosline, 1953) is greater than between many families of the great superfamily Percoidae.

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Reprinted from
ANNALS OF THE NEW YORK ACADEMY OF SCIENCES
Volume 90, Article 3, Pages 770-787
November 17, 1960

OBSERVATIONS ON CIGUATERA-TYPE TOXIN IN FISH*

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This is an interim report on the progress of an investigation of ciguatera in the tropical Pacific that is being carried on at the Hawaii Marine Laboratory of the University of Hawaii. For almost two years these studies have been supported not only through grants‡ but also through informal cooperation of the government of the United States Trust Territories, the United States Air Force, the medical services of the United States Army and Navy, and the Royal Air Force of Great Britain. This widespread support of the investigation reflects the gravity of the problem of poisonous fishes in the Pacific.

These investigations have been limited primarily to the toxin from the flesh of the large red snapper, *Lutjanus bohar* (Forskål), from the Line Islands, south of the Hawaiian archipelago. All of the later studies dealing with bioassay and chemical extraction have been confined to this species from Palmyra Island in the Line Islands. This restriction was imposed to insure that only one type of toxin was being investigated. While it is unlikely that other fishes causing ciguatera have toxins differing from those of *L. bohar* from Palmyra, this could not be assumed. *Lutjanus bohar* was selected as the fish for study because it is reported to be one of the most consistently toxic fish throughout the Pacific. It is generally abundant and easily caught, and it is large enough to provide adequate material for sampling. Palmyra Island was selected for logistic reasons and because of the high toxicity of the fishes there.

This report covers the work that has been done on the definition of the problem, the development of a bioassay, the initial attempts at extraction and purification of the toxin, and a preliminary inquiry into the relationship of ciguatera to toxin from a common alga.

Further Definition of Ciguatera

There is no need for a review of the occurrence or the symptomology of fish poisoning, nor for a general discussion of its possible origin, for this has been done adequately in the literature (Hiyama, 1943; Halstead, 1959; and Randall, 1958). It will suffice here to state that the fish of the tropical Pacific with flesh toxic to humans have been divided into five major categories: sharks, eels, scombroid fishes, puffers, and the various fishes bearing ciguatera toxin. Only two of these categories have been adequately studied: the puffers, wherein the chemistry and pharmacology of the toxin have been explored (*inter alios* by Yudkin, 1944; and Tsuda *et al.*, 1960); and the scombroid fishes, wherein the causa-

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* This paper is Contribution 136 from the Hawaii Marine Laboratory, University of Hawaii, Honolulu.

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‡ The work described in this paper was supported in part by Research Grant RG 5714 from the National Institutes of Health, Public Health Service, Bethesda, Md., Contract AT (04-3) 235 from the Atomic Energy Commission, Washington, D. C., and Contract NR 107-405 from the Office of Naval Research, Department of the Navy, Washington, D. C.

tive organism, a bacterium, has been isolated and identified (Kawabata *et al.*, 1956).

One or possibly two more types of fish toxicity have come to light in the course of this investigation. The first has been named "hallucinatory mullet poisoning" (Helfrich and Banner, 1960); it has been reported from various mullet (Mugilidae) and surmullet (Mullidae) and possibly other fish from restricted areas on the reefs of Hawaii. It may also occur at Norfolk Island in the South Pacific and in the waters of South Africa. These fish, when eaten, produce a syndrome that includes hallucinations if the patient is awake or nightmares if asleep; other symptoms, which may include itching of the mouth and throat and locomotory difficulty, are variable. The disease is distinguished from ciguatera by the rapid onset of and recovery from the symptoms, by the hallucinations, and by the lack of gastrointestinal involvement. It was established on the basis of case histories; adequate medical studies have not been made on it nor has it yet been produced in the laboratory with either test animals or human subjects.

The second type, which tentatively may be called clupeoid poisoning, appears to be widespread through the islands of the more tropical Pacific and Indian Oceans, for vague reports on it (chiefly in personal correspondence) have originated in the Marshalls, Societies, New Caledonia, Fiji, Indonesia, and Ceylon. The fish implicated is a sardinelike fish (possibly *Sardinella*) which becomes toxic only during certain seasons, as in Fiji during the *balolo*-worm season (November and December); at other times the fish may be eaten with impunity. During the toxic season it may be lethal, as in the case of the deaths of five members of a Fijian village caused by eating a sardinelike fish in December, 1955 (*Pacific Islands Monthly*, Jan., 1956). No medical details of the symptoms are available, and little else is known about the occurrence of these toxic fish. However, if they are seasonally toxic, they appear to be markedly different from fish bearing ciguatera that are consistently toxic throughout the year.

Some previous observations on ciguatera have been confirmed through personal interviews, through correspondence, and through laboratory tests. These observations include the regionality of ciguatera and the changes in the pattern of toxicity over the years.

Ciguatera has long been reported to be of regional occurrence, limited to definite islands and, possibly, to narrow regions of those islands. This type of distribution has been confirmed in the Line Islands. At Palmyra we have found by mongoose-feeding tests (see below) 95 per cent of a total of 61 specimens of *L. bohar* over 50 cm. long (taken near the channel entrance) to be highly toxic. At Christmas Island, 357 miles distant, 51 per cent of a total of 65 specimens of *L. bohar* of similar size caught to the north of the entrance to the lagoon were toxic. At Fanning Island, between Palmyra and Christmas Islands, the fish were highly toxic in 1946, but the toxicity has decreased since that time (Ross, 1947; Halstead, 1959). At Washington Island, near Fanning Island, M. N. Fagg, resident manager of the coconut plantation, wrote in a personal communication in 1959, that "there are no fish known to be poisonous at Washington. . . ." He estimates that the native population of 310 Gilbertese consume perhaps 400 to 500 lb. of fish per day, of which *Takananingo* (Gilbertese for *L. bohar*) is "eaten in quantity."

An indication of the very narrow regionality may be found in the data relating to fish caught north and south of the lagoon entrance at Christmas Island. About one half of the large fish caught to the north were toxic, yet only one of the five caught to the south of the entrance, about six miles distant, was toxic. This difference in toxicity was reported also by the Gilbertese residing upon the island.

Other authors have cited the changing toxicity over the years in specific island areas (Randall, 1958; Bartsch *et al.*, 1959; Halstead, 1959). A new and dramatic change in toxicity of fish occurred in late 1959 at Midway Island in the Hawaiian chain. Only one previous attack of fish poisoning had been known to occur there, but in 1944 about 24 persons were poisoned by eating a "black sea bass" (Lee and Pang, 1945*a*, 1945*b*); thereafter the eating of "colored" fish was discouraged by the United States Naval authorities. However the inhabitants, military and civilian, ate small "papio," *Caranx cheilio* Snyder, caught in abundance in the lagoon. This fish was esteemed and contributed regularly to the diet of many of the residents; one woman who was interviewed stated that she had eaten the fish on the average of once a week for two years. In the latter part of October, 1959, the species suddenly became toxic and in the following two months more than 25 individuals were treated for the characteristic ciguatera symptoms of varying intensity at the Naval Hospital. The present toxicity of the fish is not known, for the residents have ceased to eat this species.

TABLE 1

SPECIES OF FISH FOUND TO BE TOXIC BY MONGOOSE-FEEDING TESTS*

Species	Common name	Locations
Lutjanus bohar (Forskål)	Snapper	Marquesas Is., Line Is., Marshall Is.
Lutjanus gibbus (Forskål)	Snapper	Line Is.
Lutjanus monostigmus (Cuvier and Valenciennes)	Snapper	Society Is.
Lethrinus miniatus (Forster) Bloch and Schneider	Snapper	Marshall Is., Line Is.
Lethrinus variegatus Cuvier and Valenciennes	Snapper	Line Is.
Monotaxis grandoculis (Forskål)	Snapper	Line Is.
Plectopomus leopardus (Lacepède)	Grouper	Marshall Is.
Epinephelus fuscoguttatus (Forskål)	Grouper	Line Is.
Cephalopholis argus Bloch and Schneider	Grouper	Line Is., Society Is.
Variola louti (Forskål)	Grouper	Line Is.
Acanthurus triostegus triostegus (Linnaeus)	Surgeonfish	Line Is.
Ctenochaetus striatus (Quoy and Gaimard)	Surgeonfish	Line Is.
Caranx ignobilis (Forskål)	Jack	Marquesas Is., Line Is.
Caranx lugubris Poey	Jack	Marquesas Is.
Gymnothorax javanicus (Bleeker)	Moray Eel	Line Is.

* Identification after Schultz *et al.* (1953). Fishes of the Marshall and Mariana Islands. Bull. U. S. Nat. Mus. **1** (202).

It was not the purpose of this phase of the investigation to study the toxicity of fish other than *L. bohar*. However, incidental to the main investigation, certain fish were tested by the mongoose-feeding tests and were found to be toxic. The results are presented in TABLE 1.

All of the species cited in this table caused similar response in the test animals and the reaction varied only with the toxicity of the sample. This is notable because moray eels have been suggested to have a type of toxin distinct from that of ciguatera, yet specimens of *Gymnothorax javanicus* (Bleeker) from Palmyra caused symptoms that could not be distinguished from those caused by the other fish. This would indicate that the toxin in moray eels may be the same as that of ciguatera (see discussion of Randall, 1958), but until chemical studies are completed no positive statement can be made.

Development of a Bioassay

The studies on a bioassay may be divided into three phases: a search for a reliable quantitative feeding test, the development of a test by injection of an extract of the fish flesh, and an investigation of the reliability of a previously published test.

Based on the bioassay developed for testing *Gonyaulax* toxin in shellfish, a general test had been developed for poisonous fish that consisted of an intraperitoneal injection of an extract into mice (Ishihara, 1918; Yasukawa, cited in Hiyama, 1943; Macht & Spencer, 1941; Hiyama, 1943). The extract was either an alcoholic or an aqueous extract of the flesh or viscera. This test was used on all types of toxic fish encountered and was standardized by Halstead and his co-workers (Halstead & Bunker, 1954) who first used acidified water and later used distilled water as the extraction medium.

As the reactions in humans result from the ingestion of fish, the primary test used in this investigation was based on the reactions of animals fed potentially toxic fish.

Initially, feeding experiments were carried on with cats; however, because of legal restrictions in Hawaii, the use of cats as test animals is difficult. It was found that the mongoose, *Herpestes mungo*, an animal introduced to Hawaii, reacted with symptoms similar to those of the cat. The chief difference is that cats, when fed poisonous fish, will often regurgitate the test meal, thereby making it difficult to estimate the amount of toxic fish retained; mongooses, on the other hand, always retain all of the toxic meal. They can be fed up to 15 per cent of their body weight of raw fish directly, or they will eat dried fish or extracts that are mixed with raw eggs.

The reactions of the mongooses are also similar in some respects to those of the humans. These reactions may be classified in five stages, based on the maximal response in the mongoose within 48 hours after a single test feeding: 0, no reaction; 1, slight weakness and flexion of the forelimbs; 2, slight motor ataxia, more pronounced flexion of the forelimbs, and weakness of the hind limbs; 3, moderate motor ataxia with weakness and partial paralysis of limbs and body musculature; 4, acute motor ataxia and extreme weakness, capable of only limited movement, or coma; and 5, death.

All reactions are accompanied by a tarry, loosely formed stool; reactions 3, 4, and 5 (before death) are sometimes accompanied by excessive salivation and trembling.

While the symptoms of the disease, especially of the more acute cases, are neurological, no morphological changes in the nervous system were observed in post-mortem examinations. Post-mortem examinations of 58 mongooses killed in feeding tests revealed that the only pathological condition was a tendency to develop gastric ulcers. When this was studied further, no apparent relationship was found between the ulcers and the toxic meals; the ulcers may be the result of the encagement of wild mongooses.

Two mongooses were fed sublethal doses of toxic fish for a month; the fish used had been found to be lethal when fed in a single feeding at 10 per cent of body weight. The test mongooses were fed intermittently 1 per cent of body weight per day as required to maintain symptoms. They soon developed an arched posture, moved with difficulty, and showed other symptoms of intoxication. They also became extremely sluggish and irritable. When the symptoms became too acute, the test animals were returned temporarily to a diet of nontoxic fish. One mongoose was fed a total of 107.7 gm. (22.6 per cent body weight) of toxic fish over a 32-day period; the other was fed 81.9 gm. (20.2 per cent of body weight) over a 33-day period. At the end of the experiment, the two test animals and two controls were killed, preserved in formalin with the central nervous system exposed, and were examined by Asao Hirano, a neuropathologist with the National Institute of Neurological Diseases and Blindness Research Station at the Guam Memorial Hospital, Mariana Islands. Hirano could find no pathological change in the central nervous system. Another pathologist of the same institution, R. Wilhoite, examined other tissues and observed evidence of hepatotoxic change; however, he requested more material to confirm his observations.

Mongooses, however, are not completely satisfactory as test animals, for they come from a wild population and are biologically variable; moreover, they consume too much fish to permit the replicate testing necessary to establish an LD_{50}. A series of invertebrates and vertebrates, selected on the basis of general availability, were tested for susceptibility to the toxin. Carnivores or omnivores, such as crabs, snails, and rats, were fed fresh or dried fish directly; filter feeders or detrital feeders, such as *Paramoecium* or *Artemia*, were fed on finely-ground fish suspended in the culture; and herbivores, such as fruit flies and pigeons, were fed on finely ground fish mixed with their normal food or were force-fed. The results are presented in TABLE 2.

There is no assurance that all animals listed in TABLE 2, assuming they are susceptible to the toxin, ingested sufficient quantities of toxic fish to cause a reaction. This is especially true in those cases where the fish was suspended in the culture medium, but the difficulty of feeding them otherwise ruled them out as satisfactory test animals. Also questionable are the results of some tests where the animals, such as parakeets or mice, would avoid eating fish or fish-contaminated food. However it is notable that a number of animals have existed without ill effects from a week to several months on a diet of fish that was lethally toxic to mongooses; they include such animals as a fish (*Acanthurus xanthopterus*), the lobster and crab (*Panulirus* and *Scylla*), and the laboratory rat.

Only three of the animals tested, other than the cat and mongoose, developed recognizable symptoms. These were the white mouse, the crayfish, and the turtle. With these, other difficulties were experienced. The mouse did not eat raw fish. When dried fish was compressed into a pellet with Purina Laboratory Chow, the mouse would eat only part and scatter much more of it, thus rendering the mouse unsuitable for quantitative assay. The crayfish reacted in the same general manner as the mongoose; it would lose its ability to right itself, develop locomotory ataxia, and eventually die; however, as was the case with the mouse, it was difficult to estimate the amount ingested. The turtle was even more unsatisfactory, for its sole reaction was to withdraw within its shell; it never ate enough to cause death.

As a quantitative bioassay based on the mongoose-feeding test was not practicable for reasons cited above, and as no other animals were found that would lend themselves to a bioassay, the mouse injection test was re-examined. The principal prerequisite of this test is the extractibility of the toxin from flesh with water. This was feasible with tetrodotoxin, which is initially a water-soluble toxin, but studies by other workers (Hashimoto, 1956; McFarren and Bartsch, 1959) and at our laboratory (Banner and Boroughs, 1958) indicated that the toxin causing ciguatera could not be initially extracted with water.

A number of workers have indicated, furthermore, that the injection of aqueous extracts into mice could not be relied upon. Among these are: Hashimoto (*loc. cit.*), who worked with *Sphyraena picuda* Bloch & Schneider; McFarren and Bartsch (*loc. cit.*), who worked with various species including *Lutjanus gibbus* (Forskål) and *Lethrinus miniatus* (Forster); Goe and Halstead (1955), who reported the intoxication of a human by fish that had been shown to be nontoxic by the test; Brock and Takata (unpublished results), who worked with *L. bohar* from Palmyra; and Banner and Boroughs (*loc. cit.*), who also worked with *L. bohar*. Thus if the mouse injection test were to be used, it would have to be carefully re-examined.

During the early phases of this work it could be shown by mongoose-feeding tests that all toxin could be removed from the flesh with 90 per cent to 100 per cent ethanol. This extract, after removal of ethanol, was injected intraperitoneally into mice. While the extract would kill mice, a similar extract of a nontoxic fish, either a tuna or a Hawaiian lutjanid (*Pristipomoides microlepis* [Bleeker]) would also cause death at 1.5 to 2.0 times the lethal level of the toxic extract.

However, a more highly purified extract gave satisfactory differentiation between the toxic fish and the control. In the preparation of the six highly toxic specimens of *L. bohar* listed in TABLE 3 an average of 131 gm. of dried, ground flesh was extracted with 400 ml. of 95 per cent ethanol in a Soxhlet extractor for 24 hours; the extract was concentrated to 50 ml. The concentrate was then diluted with 150 ml. of distilled water, yielding approximately 25 per cent alcoholic solution. The resulting solution was washed with three 100-ml. portions of petroleum ether; it was discovered by feeding tests that the aqueous solution carried the toxin and that the petroleum ether extract was nontoxic. The aqueous alcoholic solution was next extracted with 300 ml. of diethyl ether in three portions, which removed the bulk of the toxin. This ethereal extract was evaporated to dryness, yielding an average of 96.7 mg. (738 mg. kg. of dried fish flesh) of residue containing the toxin.

This partially purified extract, as well as the discarded fractions, were investigated by intraperitoneal injection in a peanut oil vehicle in laboratory mice

TABLE 2

SUMMARY OF ANIMALS TESTED WITH TOXIC *LUTJANUS BOHAR*

Phylum/Class	Animal	Common names	Method of feeding*	Reaction
Protozoa/Sarcodina	*Amoeba proteus*		Suspension in culture of raw and dried flesh; v.f.	None
/Ciliata	*Paramoecium caudatum*		Same	None
Coelenterata/Anthozoa	*Fungia scutaria*	Mushroom coral	Pieces of raw flesh; v.f.	None
Platyhelminthes/Turbellaria	*Planaria* sp.		Same	None
Aschelminthes/Rotifera	(Various genera)		Suspension in culture of dried flesh; v.f.	None
Arthropoda/Crustacea	*Artemia salina*	Brine shrimp	Same	None
	Daphnia sp.	Water flea	Same	None
	Atya bisculcata	Stream shrimp	Pieces of raw flesh; v.f., f.f.	None
	Leander debilis	Marine shrimp	Same, v.f.	None
	Macrobrachium sp.	Stream shrimp	Same	None
	Procambarus clarki	Crayfish	Same	Paralysis to death
	Panulirus japonicus	Spiny lobster	Same	None
	Paribaccus antarticus	Slipper lobster	Same	None
	Portunus sanguinolentus	Swimming crab	Same	None
	Scylla serrata	"Samoan" crab	Same	None
	Pseudosquilla ciliata	Mantis shrimp	Same	None
/Insecta	*Periplaneta* sp.	Cockroach	Pieces of dried flesh; v.f.	None
	Dermestidae	Dermestid beetle	Same	None
	Musca sp.	House fly	Pieces of raw flesh; v.f.	None
	Calliphoridae	Blow fly	Pieces of raw flesh, fresh to putrescent; v.f.	None
	Drosophila sp.	Vinegar or fruit fly	Alcoholic extract mixed in culture medium; v.f.	None
Mollusca/Gastropoda	*Achtina fulica*	African land snail	Pieces of raw flesh; v.f.	Questionable
/Pelecypoda		Various clams	Suspension of ground flesh into incurrent syphon	Expulsion of suspension
Echinodermata/Echinoidea	*Tripneustes gratilla*	Sea urchin	Raw flesh; v.f.	None
Chordata/Osteoichthyes	*Lebistes reticulatus*	Guppy	Pieces of dried flesh; v.f.	None
	Xiphophorus helleri	Swordtail	Same	None
	Pranesus insularum	Silversides	Pieces of raw flesh; v.f.	None
	Acanthurus xanthopterus	Surgeon fish	Same	None

TABLE 2—(*Continued*)

Amphibia	*Bufo marinus*	Toad	Pieces of raw flesh; f.f.	None
Reptilia	*Pseudomys scripta elegans*	Gecko	Same	None
	Leticlodactylus lugibris	Painted turtle	Pieces of raw flesh; v.f.	General withdrawal
Aves		Parakeet	Alcoholic extract evaporated on food; v.f.	None
		Pigeon	Pieces of raw flesh; f.f.	Regurgitation
		Chicks	Ground dried flesh; v.f.	None
Mammalia		Rabbit	Pieces of raw flesh; f.f.	None
		Guinea pig	Same	None
		Laboratory rat	Pieces of raw and dried flesh; v.f.	None
		Laboratory mouse	Pieces of raw flesh; v.f., f.f.	Variable reaction

* v.f., voluntary feeding; f.f., force feeding.

(closed colony Carworth Farms Webster strain). Mice weighing between 19 and 21 gm. were used. It was found that the petroleum ether extract and the aqueous alcoholic residue from both toxic and nontoxic fish would cause death in mice when injected at a level of 3.0 to 5.0 mg./gm. of mouse weight. However, the ethyl ether extract from toxic fish would produce kills at the level of 0.2 mg./gm., while the ether extract of the control (*P. microlepis*) caused no symptoms at 1.5 mg./gm., or seven times the lethal level of the toxic fish.

TABLE 3

EVALUATION OF BIOASSAY METHODS FOR TOXIN FOUND IN *LUTJANUS BOHAR*

Preparation of Extracts, Testing Methods, and Classification of Response as Discussed in the Text

Specimen	Mongoose-feeding test Response vs. per cent body weight				Intraperitoneal injection in mice						
					Water extract (5 mice used for each specimen)	Diethyl ether extract, in mg. extract/gm. mouse. Figures represent mean time to death in minutes of two mice tested at each level					
	5	10	10	15		0.1	0.3	0.5	0.7	1.0	1.5
Highly toxic											
1	2	3	4	3	N.D.[*]	(348)[†]	189	130	63	—[‡]	—
2	4	5	4	5	N.D.	(1627)	249	155	111	69	89
3	5	5	4	5	N.D.	N.D.	240	81	90	43	30
4	2	3	4	5	N.D.	(360)	90	44	63	62	43
5	2	3	4	4	N.D.	N.D.	261	139	78	72	49
6	5	3	5	4	N.D.	308	128	101	89	—	—
Moderately toxic											
7	—	—	1	1	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.	—
8	2	1	2	2	N.D.	N.D.	788	850	108	—	—
9	—	—	1	2	N.D.	N.D.	(2800)	750	—	124	—
10	—	—	1	2	N.D.	N.D.	—	N.D.	—	(367)	—
11	—	—	0	1	N.D.	N.D.	N.D.	1252	—	1044	—
12	—	—	1	0	N.D.	N.D.	N.D.	(1620)	—	—	—
Nontoxic											
13	—	—	—	0	N.D.	N.D.	N.D.	N.D.	—	2800	—
14	—	—	—	0	N.D.	N.D.	N.D.	N.D.	—	N.D.	—
15	—	—	—	0	N.D.	—	N.D.	N.D.	N.D.	N.D.	N.D.
16	—	—	—	0	N.D.	—	N.D.	N.D.	N.D.	N.D.	1000
17	—	—	—	0	N.D.	—	N.D.	N.D.	N.D.	N.D.	—
Pristipomoides microlepis (control)	0	0	0	0	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.

[*] N.D. signifies no deaths in the 72-hour test period.

[†] Figures in parentheses are times to death in one mouse of pair tested, the other living through test period.

[‡] Dash indicates no tests made at this level.

The symptoms produced in the mouse by injection were quite different from those found in the mongoose after ingestion. The mice would develop immediate diarrhea and later would become inactive and display excessive salivation and lachrymation, but they would show no paralysis; immediately prior to death the mice would display convulsive spasms for a few moments. On gross autopsy the only observable disorder was a pulmonary congestion. This difference in reaction raised the question whether the same toxin was being tested by the two methods.

Therefore, mice were fed toxic extracts, and mongooses were given intraperitoneal injections of the extract. Whether the mice were fed dried toxic fish mixed with their food or toxic extracts mixed with their food they would die showing symptoms similar to those elicited by injection; to achieve a response equal to that obtained by injection required a dosage that varied from at least equal to twice the injected amount. When the extract was mixed with egg and fed to mongooses, or when it was injected into mongooses, they would die with the same response that they would exhibit after eating raw toxic fish. The difference in symptoms was thus demonstrated to be a difference in reaction of two species to the same toxin.

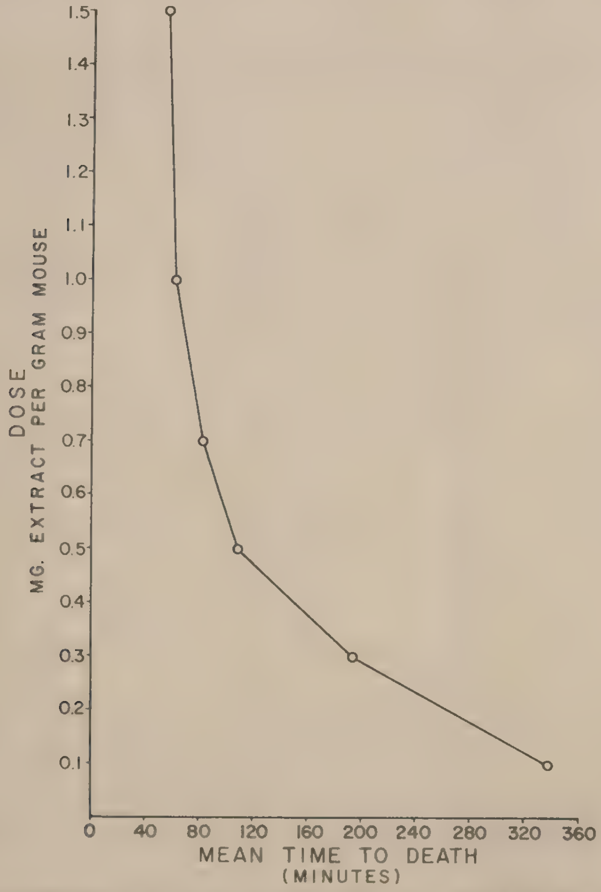

FIGURE 1. Mean time to death in mice injected at six dose levels with diethyl ether extracts of six highly toxic *L. bohar*, as shown in TABLE 3.

In order to determine the effects of size of mice on the reactions to a standard dosage, mice ranging in size from about 10 gm. to 30 gm. in five weight groups were injected with standard dosages of a mixture of highly toxic fish at a level of 1 mg./gm. of mouse. The time to death is given in TABLE 4, and the averages show that both the smallest and the largest mice are less sensitive and more variable in their reaction than are those in the 20 to 25 gm. range. The variability in time to death is given in TABLE 5.

TABLE 4
RESPONSE OF MICE OF VARYING SIZES TO STANDARD TOXIC DOSAGE IN WATER AND OIL VEHICLES
All mice injected intraperitoneally with 1 mg./gm. mouse of standard toxic mixture

Oil vehicle				Water vehicle			
Mouse weight (gm.)	Average weight (gm.)	Time to death (min.)	Av. time to death (min.)	Mouse weight (gm.)	Average weight (gm.)	Time to death (min.)	Av. time to death (min.)
9.0	9.6	66	79.7	10.1	9.4	—	103.3*
9.6		63		8.8		58.5	
9.5		97		10.1		166.5	
10.2		67.5		8.4		87.5	
9.6		105		9.5		101	
14.3	14.2	59.5	72.6*	14	14.9	48	57.0*
14.6		60.5		15.1		—	
14.1		—		14.8		50	
14.1		59.5		15.5		62.5	
13.8		111		15		67.5	
20.4	21.6	72	66.8	20	19.7	55.5	55.6*
18.9		65		19.6		61	
19.7		64		20		51	
20.3		65		19		—	
19.5		68		20		55	
23.7	24.0	62	61.6	25	24.8	60	51.3
23.8		68		25		43	
23.4		59.5		25		57	
24.0		59		25		51.5	
24.9		59.5		24		45	
32.2	31.1	71	78.8	32.9	32.9	68	66.3
31.5		74.5		32		70	
29.6		91		33.8		61	

* In some cases one mouse did not die within the test period of 3 hours; in these cases the average is based on the 4 mice that died.

At the same time that the reaction of mice of various weights was investigated, the response of mice to the toxin in a water vehicle instead of an oil vehicle was explored. The thick oil resulting from the evaporation of the diethyl ether extract was mechanically stirred with water until a stable emulsion was achieved. This emulsion, when injected intraperitoneally, produced a weight-response curve similar to that obtained with an oil vehicle, but indicated a slightly shorter time to death in all except the 10-gm. group.

The reliability of the mouse injection test was further explored in conjunction with the water-extraction test and with the mongoose-feeding test. Three groups of five specimens of *L. bohar* from Palmyra were used, representing highly toxic, moderately toxic, and nontoxic fish, as established by mongoose-feeding tests. To determine toxicities each fish was individually fed to a number of mongooses. In the highly toxic category, one mongoose was fed at 5 per cent body weight, two at 10 per cent body weight, and one at 15 per cent body weight; if at least one animal displayed a grade 4 response at 10 per cent body weight feeding, the fish was classified as highly toxic. For moderately toxic fish, the criterion was no greater than a grade 2 response at a 15 per cent body weight feeding. Because the available nontoxic *L. bohar* were much smaller in size, only a single feeding at 15 per cent body weight was possible; this produced no symptoms.

The tests based on injection of a water extract of the flesh were carried out by a modification of the published procedure of Halstead and Bunker (1954).

TABLE 5

VARIABILITY IN TIME TO DEATH OF THE MICE GIVEN IN TABLE 4

Sample size	Vehicle	Av. weight (gm.)	Mean time to death (min.)	Standard deviation of time to death (in sample)
5	Oil	9.6	79.7	19.72
4	Water	9.4	103.3	45.66
4	Oil	14.2	72.6	25.58
4	Water	14.9	57.0	9.50
5	Oil	21.6	66.8	2.88
4	Water	19.7	55.6	4.24
5	Oil	24.0	60.4	3.70
5	Water	24.8	51.3	7.36
3	Oil	31.1	78.8	10.68
3	Water	32.9	63.0	4.73

Two ml. of distilled water and 1 gm. of fish flesh were homogenized in a blender for 2 min.; this slurry was then centrifuged at 2000 rpm (900 g) for 25 min. One milliliter of the clear supernatant fluid was injected intraperitoneally into each of four mice weighing 15 to 25 gm. Reactions were observed for 26 hours and placed into four groups: immediate death; immediate symptoms and delayed death; immediate symptoms and recovery; no symptoms.

The following changes were made in the Halstead and Bunker technique: (1) 25 gm. of fish flesh were used in all cases; (2) the container of the blender was cooled to assure temperatures below 40° C., which prevented excessive precipitation of proteins; and (3) the resulting slurry was first centrifuged for 5 min., then decanted and recentrifuged as specified by Halstead and Bunker.

The diethyl ether extracts were prepared as outlined above; all were injected intraperitoneally in a peanut oil vehicle.

In addition to the three groups of *L. bohar*, a control was run with *Pristipomoides microlepis* from the Honolulu fish market.

The results are presented in TABLE 3; the accompanying graph (FIGURE 1) shows the curve of the mean time to death of the mice injected with varying amounts of the highly toxic group shown in the table.

The mongoose-feeding test and the injection tests of water and diethyl ether extracts were tried on a specimen of *Caranx ignobilis* (Forskål) that had caused mild ciguatera in a human. This jack (or pompano or ulua) weighed 38 lb., and was caught in the lagoon entrance at Palmyra. A large portion, possibly 2 lb., was baked and eaten by an individual who later developed a characteristic itch of the mouth and skin, a sensitivity in the hands to heat and cold, and some "difficulty" in the leg muscles that manifested itself by pain and fatigue, especially when climbing stairs. Other members of the victim's family who ate smaller portions noticed no symptoms. The uncooked portions, saved in a frozen condition, were fed to mongooses at 5, 10, and 15 per cent body weights; there was no reaction at 5 per cent, marginal reaction (grade 1 response) at 10 per cent, and slight reaction (grade 2 response) in two mongooses at 15 per cent. There was no reaction to the injection of the water extract in five mice. The diethyl ether extract was injected in an oil vehicle at 0.1, 0.5, 1.0, 1.5, 2.0, 2.5, and 3.0 mg. of extract per gm. of mouse. No deaths resulted from the lower three injection levels; 2 of 4 mice died at 1.5 mg. gm., and all died at the three higher levels; in the three uppermost injection levels the average times to death were 98, 36.5, and 34.5 min., respectively.

While the systematic LD_{50} was not determined for adequate numbers of mice to establish a truly quantitative response for the diethyl ether extract, the following conclusions may be drawn:

(1) Feeding tests with mongooses may be used for qualitative determination of toxicity in *L. bohar*, but there is too much variation in the animals to permit reliance on the reactions of one or two mongooses to establish the degree of toxicity.

(2) The published technique of Halstead and Bunker (*loc. cit.*) of injection of a water extract of the flesh of *L. bohar*, and probably also of *C. ignobilis*, gives no indication of the toxicity of the fish. If other types of fish that have been characterized as causing ciguatera have the same toxin as *L. bohar*, it is most unlikely that this test will give a reliable indication of their toxicity.

(3) The injection of a partially purified diethyl ether extract, as outlined above, presents the most reliable method by which to test for toxicity in *L. bohar*. This method is likely to produce quantitative results once the assay is standardized with large numbers of test fish and test animals and is based on LD_{50} data.

Initial Attempts at Isolation of Toxin

At this time it is not possible to report fully on the isolation of the toxin. However, a brief review of the initial isolation and purification studies of the toxin will be presented.

First, a possible decomposition or loss of the toxin in the course of air-drying the flesh at 90° C. was explored. Replicate mongoose-feeding tests with raw and dried *L. bohar* indicated that there was no loss of toxicity; this confirmed an earlier finding by Banner and Boroughs (1958).

Second, the extractability of the toxin by various solvents was investigated. Thirty gm. of a uniform mixture of dried toxic *L. bohar* were extracted with different solvents, usually with two successive portions of 60 ml. each. The solvent was evaporated to dryness and the residue weighed. The combined extraction residues and the extracted fish flesh, after complete removal of solvent, were fed to mongooses separately. The results are shown in TABLE 6.

TABLE 6 shows, *inter alia*, that ethyl alcohol was the extraction solvent of choice. In order to determine the most efficient method of alcohol extraction of the maximum amount of toxin from the flesh, three methods were explored. In the first, 100 gm. of dried flesh were extracted with hot ethanol in a blender with three portions of 200 ml. each for 5 min.; after solvent removal the combined extracts produced 4.27 gm. of extractable matter. Then the residual fish flesh was re-extracted with ethanol in a Soxhlet for 16 hours, which removed an additional 7.79 gm. of extract. Mouse injection tests showed that both blender and Soxhlet extracts contained toxin.

TABLE 6

EFFICIENCY OF VARIOUS SOLVENTS IN EXTRACTING TOXIN FROM DRIED FLESH OF *LUTJANUS BOHAR*, AS INDICATED BY MONGOOSE-FEEDING TESTS

Solvent (reagent grade)	Extracted (gm.)		Reaction to	
	1st Extraction	2nd Extraction	Extract	Residue
Water	4.35	*	None	2, 3
Ethanol, 90%	1.15	1.06	3	None
Ethanol, 100%	1.29	0.45	5	None
Methanol	1.52	0.94	None	2
Butanol	0.74	0.23	None	†
Acetone	0.25	0.10	2	None
Chloroform	0.30	0.13	2, 3	None
Diethyl ether	0.27	0.01	3, 4	None
Benzene	0.27	0.04	None	None
Petroleum ether (B.P. 30–60° C.)	0.21	0.02	None	3

* Single extraction only.
† Not tested.

Third, Bligh and Dyer's (1959) triple solvent extraction method was tried, but it was found that this method also failed to extract much of the toxin that could subsequently be removed by Soxhlet extraction with alcohol. Therefore the best method found to date to remove the toxin is by Soxhlet extraction.

After the elaborate purification method, outlined under the section on bioassay, had been developed, an abbreviated method was tried, wherein the dried flesh was extracted directly with diethyl ether, thus bypassing the extraction with alcohol and the washing with petroleum ether. Here it was found that the diethyl ether extract of the toxic fish was not as toxic in terms of mg. gm. lethal dose in mice as that obtained by the elaborate method, and furthermore that the nontoxic control fish (*P. microlepis*) would kill mice at nearly the same dose levels.

Further purification of the diethyl ether fraction cannot be reported upon at this time, but it may be stated that through the use of column chromatography with solvents of varying polarity, a noncrystalline but possibly homogenous extract has been isolated. The yield of this extract is 32 mg./kg. of wet flesh extracted from highly toxic fish; this extract, when injected into mice at 65 γ/gm., will kill in 14 min.

Relation of Ciguatera to Toxin from Lyngbya majuscula

Various authors (Dawson *et al.*, 1955; Randall, 1958; Dawson, 1959) have suggested that the toxin of ciguatera is passed through the food chain to the large carnivores, and that its ultimate source may be a blue-green alga. It has further been suggested that the source may be algae of the genus *Lyngbya*, a widespread form known to be toxic.

During the summers of 1958 and 1959 there were outbreaks in Hawaii of a "swimmer's itch" produced by strands of *Lyngbya majuscula* Gomont that had become entangled in close-fitting swimmer's trunks. During the summer of 1959, workers at the Hawaii Marine Laboratory investigated the spread of dermatitis-producing *L. majuscula* (Banner, 1959), which presented a public health problem. At the same time the *Lyngbya* toxin was compared, in a preliminary way, with the toxin that produced ciguatera from *L. bohar.*

L. majuscula would produce severe and persistent blisters and later lesions of the skin when it was applied in a patch test for 6 to 18 hours (FIGURE 2). The same alga when dried and mixed with mouse food would kill test mice that ate the food. When an alcoholic extract was made and injected intradermally in guinea pigs and rabbits, it would cause erythema and vesicular eruptions; the alcoholic extract when evaporated on mouse food would kill mice.

Not all strains of *L. majuscula* about the island of Oahu were toxic. For example, the alga from Laie and Kailua, two beaches on Oahu about 22 miles apart, was toxic during both summers, but the same species from Kaneohe Bay, located between Laie and Kailua, proved to be consistently nontoxic by skin tests.

Possible relationship of the toxins from *Lyngbya majuscula* and from *L. bohar* was investigated in three ways:

(1) *Solubilities.* While great caution must be exercised when one compares the solubility of a given component that may be present in two mixtures of widely differing composition, nevertheless the toxins from the fish and the alga appear to have different solubility characteristics. The toxin from both the alga and the fish could be extracted with 90 and 100 per cent ethanol, but the toxin from the alga could also be extracted with hot water or cold petroleum ether, although not as efficiently as with alcohol. The toxin from *L. bohar*, on the other hand, could not be extracted with either of these solvents. When the ethanol extract from the alga was purified in a manner parallel to that used for *L. bohar*, as outlined previously, some of the toxin appeared in the petroleum ether washing, as well as in the diethyl ether fraction.

(2) *Patch tests.* Alcoholic extracts of *Lyngbya* would produce erythema and blisters when applied as patch tests to human subjects; similar extracts of *L. bohar* caused no reaction.

(3) *Geographic spread of both conditions. Lyngbya* dermatitis has been known in Hawaii by scientific observation for at least two years, and much longer by

accounts of fishermen. However, in Hawaii only two cases of fish poisoning of the ciguatera type have definitely been established. In both cases the fish was not caught near known areas of toxic *Lyngbya*. The toxic seaweed areas, on the other hand, are heavily fished for many species of fish. Moreover at Palmyra, where the percentage of fish bearing ciguatera is very high, none of the *L. majuscula* tested produced any reaction in skin tests. It is worthy of note that Habekost *et al.* (1955) found algae from Palmyra (including *L. majuscula*) to be toxic by their tests using intraperitoneal injection of purified aqueous extracts of the algae.

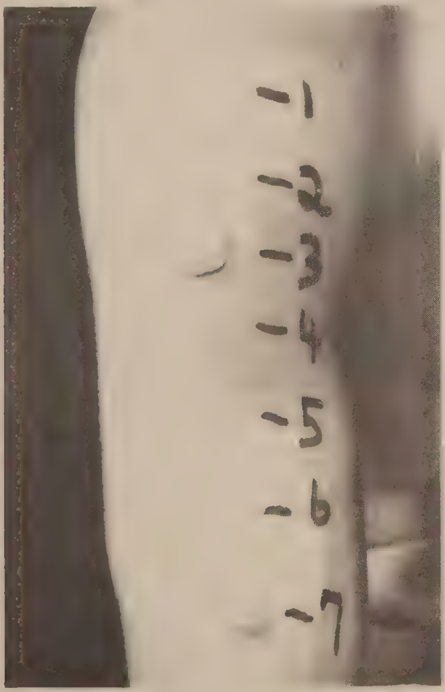

FIGURE 2. Reaction in a 6-hour patch test to *Lyngbya majuscula* Gomont. Upper arm of subject showing the results of seven samples of *L. majuscula* collected from swimming beaches about the island of Oahu, Hawaii. Note that in addition to the conspicuous blister from samples 3 and 7, there is a mild reaction to sample 4.

It appears, therefore, from these initial considerations that the compound or compounds from some strains of *Lyngbya majuscula*, which cause dermatitis, are chemically not identical with the toxin that produces ciguatera from the ingestion of *L. bohar*.

Summary

(1) Ciguatera should be distinguished from hallucinogenic mullet poisoning and possibily from a yet-undescribed condition resulting from eating seasonally toxic fish.

(2) The narrow regionality of fish causing ciguatera and the changing patterns of toxicity in the central Pacific have been further confirmed.

(3) Fifteen species of fish causing similar reactions in feeding tests are listed; the validity of the separation of *Gymnothorax* poisoning from ciguatera is questioned.

(4) Two methods of bioassay for ciguatera-producing fish are presented, based on *Lutjanus bohar*, a red snapper from Palmyra Atoll. The first is a feeding test using mongooses as test animals; the second, which shows good potential to become a quantitative test, is based on the intraperitoneal injection into standard mice of an alcoholic extract of fish flesh, subsequently purified by washing with petroleum ether and re-extraction with diethyl ether.

(5) More than 37 species of invertebrates and vertebrates were tried for possible use in feeding tests for bioassay; of these only three, a crayfish, a turtle, and a laboratory mouse, reacted.

(6) A previously used test, which has been the criterion of toxicity in numerous toxic fish surveys, was found to be unreliable for the fish used in this study.

(7) A procedure is given for the initial extraction and purification of the toxin from fish flesh. Discussion of eventual isolation of the pure toxin has been reserved for further experimental confirmation.

(8) The appearance of a strain of *Lyngbya majuscula* that produces dermatitis in humans upon contact is discussed, together with its possible relationship to ciguatera from fish; it was concluded that there is at present no evidence that the toxins from the alga and from the fish are identical or even similar.

Acknowledgments

We thank the following individuals and institutions for their cooperation: William A. Gosline, University of Hawaii, and Donald W. Strasburg, United States Fish and Wildlife Service, Honolulu, Hawaii, for aid in the identification of fish; Emmett G. O'Donnell and Edwin S. Chickering, United States Air Force, for arrangements to visit Palmyra Atoll; D. H. Nucker, of the United States Trust Territory of the Pacific Islands, for aid in obtaining fish from the Marshall Islands; George W. Chu, University of Hawaii, for suggestions on the study of *Lyngbya*; James Mead, University of California Medical Center, Los Angeles, Calif., for valuable advice on methods of lipoid purification; Asao Hirano and R. Wilhoite, Guam Memorial Hospital, Guam, for pathological studies; James K. MacNamee, United States Army, for furnishing the laboratory mice; Hope Gray and Leoniece A. Baer for assistance in the laboratory; the United States Fish and Wildlife Service and the Hawaii State Board of Agriculture and Conservation for aid in obtaining specimens; and the personnel of the British Royal Air Force base at Christmas Island for permission to visit Christmas Island and for their aid in obtaining specimens there.

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Reprinted from THE ELEPAIO, Vol. XXI, No. 3, September 1960
Journal of the Hawaii Audubon Society

THE BLACK-HEADED MANNIKIN, LONCHURA MALACCA ATRICAPILLA A NEW BREEDING BIRD ON THE HAWAIIAN ISLANDS

By Miklos D. F. Udvardy[1, 2]

On April 24, 1959, while studying the bird fauna of Oahu in the vicinity West Loch, Pearl Harbor, I found a favorite watering place of the birds amongst the dry kiawe woods and cane fields. The exact locality was between Honouliuli and the abandoned military camp near West Loch, to the west of the Waipahu-Ewa Beach highway, 0.8 miles from the "Barbers Point Housing Development."

Among the birds that came to drink and bathe, were two kinds of strange passerines. The conspicuously coloured, chestnut and black birds with pale beak were easy to recognize as the Black-headed Mannikin, Lonchura malacca atricapilla (synonymous with L. ferruginosa, Chestnut Mannikin, Black-headed Nun, or Black-hooded Nun), while the other small weaver finch, reddish tan in colour with dark and white markings on the head seemed more of a puzzle.

On April 25, I spent more time observing the birds of the waterhole and identified the latter birds as fledged young of the Black-headed Mannikin.

Field identification. When seen from about 30 feet away with 10 power binoculars, the adults of these very active birds seemed to be of the size of the Ricebird (Munia risoria Temm.) and to have the same upright posture when sitting on a branch or grass stalk. The head and lower parts are black, the wings, tail and upper parts dark chestnut-rufous red. The beak is conspicuously white looking, at closer glance, bluish horn-colored. The wary birds all turn toward the observer showing their black head and underside, while those farther away look predominantly chestnut-red. Thus watching a flock, the observer gets the impression that he sees some black and some red birds.

The adults in flight are conspicuously dark, blackish birds. They have an undulating flight, similar to that of the ricebird, and birds of the flock keep fairly close together. The contact call in flight - adults and fledglings use it alike - is a high pitched, staccato whistle, in frequency and pitch reminiscent of the contact call of the Red crossbill (Loxia curvirostra).

The fledglings I saw were of near adult size, and had the same posture and flight. The under side is dark ochre, the wings and the upper part of the bird darker, and rufous ochre (tan) more rufous on the crown and nape, and rufous red on the tail. The forehead and the lores around the beak are dark, the beak dark

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1. Contribution No. 137 of the University of Hawaii Marine Laboratory.
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horn-colored, and the whitish edge of the mouth is conspicuous, forming a white stripe with the surrounding dark feathers on these fledglings.

Behavior. The mixed flock of adults and young came to the temporary waterhole about every 40 minutes between 1100 and 1300 hours on April 25, and appeared at the same place on April 26 once between 0805 and 0930 hours. They came flying through half-grown sugar cane fields, from the direction of a Kiawe thicket, with grassy clearings, about 400 yards away. The flock circled the waterhole several times before settling on the bushes where they mixed with ricebirds. The latter species also had fledglings, and on April 26, a Black-headed mannikin fledgling was observed begging food from an adult ricebird. The birds were quite wary. They did not let me closer than about 30 feet unless stalked behind cover, and did not alight at the waterhole when I was exposed.

Habitat. The waterhole where the birds were observed was the only watering place left in the irrigation ditches of the cane fields. It was surrounded by half an acre of kiawe stand with dense brush and grassy understory. Several kiawe woodlots were within half a mile distance, and I suspected that the Mannikins came from these woods, but I searched there for them in vain. The bird fauna around the waterhole was as follows on April 24 - 26:

Ring-necked pheasant
Golden plover
Lace-necked dove
Barred dove
Short-eared owl
Mynah
White-eye
Strawberry finch
Black-headed mannikin
Ricebird
English sparrow
Red cardinal
Brazilian cardinal
House finch

Occurrence. The following extract from my notebook gives the only known observations of the Black-headed mannikin. The locality of all observations is the above described area.

Date		
April 24, 1959	8 adult	8-10 young
April 25, 1959	8 adult	10 young
April 26, 1959	10 adult	15 young
May 16, 1959	10 adult	12 young
May 19, 1959	0 adult	4 young
May 23, 1959	None seen, but contact calls heard. The waterhold was dry.	

Origin. The Black-headed Mannikin was introduced as a cage bird to the Hawaiian islands between 1936 and 1941 (E. H. Bryan, Jr. in lit.). I saw specimens of it in 1959 in tow Honolulu pet shops, where they were called "Black-hooded nun." On inquiry, I was informed that the birds are imported from the port of Calcutta, India. Thus the wild flock at Ewa evidently originated from escaped cage birds. If the flock originated from one pair, the present number of adults suggests that they must have been free for two years. While they apparently bred successfully in 1959, and they seemed to thrive in the habitat of their close relatives, the ricebird and the strawberry finch, we still have to see

whether these handsome birds will spread further on the islands in the coming years.

Status in the Hawaiian avifauna. The following addition should be made to the check list and summary of the Hawaiian Birds (Bryan, E. H., Jr. 1958, Honolulu. p.24). Family: Ploceidae - 221A. Lonchura malacca atricapilla. Black-headed Mannikin. Introduced as a cage bird; escaped and breeds on Oahu. Juvenile male on May 16, 1959, at Ewa, Oahu (Bernice P. Bishop Museum, Honolulu, Acc. No. 5585.

Acknowledgements. I am grateful to Messrs. C. E. Reppun, M. Takata and R. Warner of the Territorial Board of Agriculture and Forestry, Honolulu, for the collecting permit I obtained; to Dr. Jean Delacour, Los Angeles, for information about the taxonomic status of the Mannikins; to the University of Hawaii Marine Laboratory for providing transportation to the field; to the National Research Board of Canada for supporting my Hawaiian field studies.

Reprinted from THE ELEPAIO, Vol. XXI, No. 4, October 1960
Journal of the Hawaii Audubon Society

MOVEMENTS AND CONCENTRATIONS OF THE HAWAIIAN COOT ON THE ISLAND OF OAHU

By Miklos D. F. Udvardy[1], [2]

Very little is known about the present status and seasonal movements of the Hawaiian coot (Alae Keokeo), Fulica americana alai Peale, still a common breeding bird of the freshwater marshes, ponds and canals of the main Hawaiian islands. Schwartz and Schwartz, in a publication of 1952 (Schwartz, C. W. & E. R., Auk 69:446), stated that the species is non-migratory and has no obvious seasonal movements. They made no census or estimate of the breeding population on any one of the islands.

Such a census would be difficult to accomplish, since the breeding places of the coot are quite scattered on small ponds, reservoirs and irrigation ditches. There are, however, a few larger pond and marsh areas on Oahu where the coot population shows marked fluctuations; by regular and simultaneous census, the nature of their seasonal and annual movements and fluctuations could easily be revealed.

There were three principal areas of coot concentration on Oahu in 1958/59 [3], follows: The Kahuku marsh near the northern point of the island; the Kaelepulu marsh, on the west, drastically reduced in size by draining and filling operations during early 1959; and Salt Lake in the south, between Honolulu and Pearl Harbor. Smaller areas of concentration, apparently not equally utilized every year, are Kahana Bay and Nuupia ponds on the windward side, Kuapa pond and the Waipahu tidal marshes in the south, and some bigger reservoirs in the interior of the island.

At Kahuku, the reservoir of the irrigation system and the marsh slough near the abandoned airfield had no coots on Oct. 21, Nov. 4, 20, 27, Dec. 4, 1958 (MDFU) and Jan. 25 (MacClellan, M. W., Elepaio 19:57, 1959) and Feb. 20, 1959. On April 21, 1959, there were 80 coots on the reservoir and several adults as well as two broods of downy chicks on the neighbouring irrigation ditches. On May 1, 1959, the reservoir had about 60 coots. The water level of this reservoir is regulated according to the need of the sugar industry and during the winter it contained little or no water. It is significant for the other areas under consideration that the coot left the Kahuku area entirely for the winter, and returned for the spring nesting season, at which time both the ditches and the pond were utilized.

The 300 acre Kaelepulu marsh was almost dry, with water only on some 50 acres, during the early fall of 1958. On August 3 (Pyle, R. L., Elepaio 19:17, 1958), Oct. 7 and 28, 1958, no coots were in this area. After the pond gradually filled

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[1] Contribution No. 138 of the University of Hawaii Marine Laboratory.

[2] These studies were also aided by a grant of the National Research Council of Canada.

[3] All observations, unless a reference is quoted, were made by the present author (MDFU).

up, coots concentrated here (Oct. 30, 80 birds; Nov. 20 and 27, 350 birds estimated). On Dec. 11 no coots were seen, on Dec. 21, however, A. Stoops (Elepaio 19:48, 1959) recorded 200 birds again, and on January 8, 1959, I counted 155 coots. On April 30, 1959, and consecutive visits I found that the nesting habitat of the coots was mostly destroyed and no birds were seen though possibly some nested in the shelter of the remaining marshy vegetation.

In the past records of this marsh, a sudden increase of coots is shown by the estimation of 200 birds on Dec. 29, 1946 (Delamere, C. et al., Elepaio 7:49, 1947) and over a thousand a few days later (Jan. 4, 1947: Donaghho, W. R.,Elepaio 7:55, 1947) and on Feb. 15, 1947 (Kleen, R., Elepaio 7:59, 1947). On April 7, 1947, Schwartz & Schwartz (L.c.) still found the same number of coots.

Salt Lake, a water body with no emergent vegetation, filling a sunken crater of over 200 acres in size, shows the greatest recent concentrations of coots during the winter half of the year. Three series of observations from the literature complement my field notes of 1958/59, and all of these are found in Table I.

Table I. Serial Observations of Coot on Salt Lake, Oahu

Date	No. of Coots	Reference
Nov. 13, 1955	225	Wilson, E., Elepaio 16:37, 1956
Dec. 26, 1955	108	Rockafellow, R. et al, Elepaio 16:38, 1956
Jan. 29, 1956	42	Gossard, G., Elepaio 16:52, 1956
Feb. 12, 1956	0	Anon., Elepaio 16:53, 1956
Dec. 22, 1957	600	Hanson, C., Elepaio 18:48, 1958
Jan. 26, 1958	1000	Labrecque, A., Elepaio 18:62, 1958
Nov. 4, 1958	200	MDFU
Nov. 15, 1958	800+	"
Dec. 9, 1958	500+	"
Dec. 21, 1958	2002+	" (Cf. Rockafellow, R., Elepaio 19:47, 1959)
Dec. 27, 1959	806	Hanson, C., Elepaio 20:52, 1960
Jan. 10, 1960	400+	Stephenson, F. L., Elepaio 20:66, 1960
May 22, 1960	1000	Mench, M., Elepaio 21:6, 1960

The Christmas censuses of the Hawaii Audubon Society (all published in tabulated form in the volumes of Elepaio, therefore no further reference will be given) also indicate substantial annual fluctuation of coots on the two discussed areas as Tables II and III will show.

Table II. Estimated Number of Coots on Kaelepulu - Christmas Counts

Year	No.	Year	No.	Year	No.
1944	421 *	1949	486	1955	91
1945	231 *	1950	628 **	1956	0
1946	200 *	1952	653	1957	538 ***
1947	105	1953	0	1958	200
1948	883	1954	120	1959	327

* Kalihi and Kauainui areas included
** Kuapa pond included
*** Kailua area included

Table III. Estimated Number of Coots on Salt Lake, Christmas Counts

Year	No.	Year	No.
1954	303	1957	600
1955	108	1958	2002
1956	208	1959	806

We see from these tabulations that the 15 annual Christmas censuses at Kaelepulu, and those of six consecutive years at Salt Lake, show violent fluctuations, with an all time peak at Salt Lake in 1958. Where the observations are simultaneous, i.e. from 1954 to 1959, the annual fluctuations are neither coincident, nor complementary. Thus these two winter habitats do not seem to have a common denominator.

Serial observations and the range of the Christmas census results indicate that coot numbers at Kahuku and Kaelepulu fluctuate partly under the influence of the availability of the habitat. This is not the case at Salt Lake which is not a substantial breeding area for the coot to my knowledge, and in which no habitat changes were noted during my period of observations. Salt Lake may have an especially attractive source of food for coots during certain periods of the winter, or else it draws flocks of coots from nesting areas that during the winter are temporarily unsuitable for the birds (such as, e.g. the Kahuku area was during 1958/59).

I have considered the possibility of population exchange between Kaelepulu and Salt Lake. However, the coot population at Kaelepulu had two peaks and three lows during 1958/59, and these coincided with the two peaks and two lows observed at Salt Lake. Therefore an exchange is not likely. My observations at the latter locality were unfortunately not maintained after December 1958, since I did not realize at once the significance of the remarkable build up of the population during the fall.

Summing up, the large winter concentrations seem to mean fairly regular seasonal movements of the Hawaiian coot. They could be brought about by aggregation from scattered habitats, by influx from other islands, or by influx from outside sources.

While movements of coots from island to island were known in the past (G. C. Munro, /Birds of Hawaii, Honolulu, 1944. p. 54/ reports that Niihau coots migrate away when the ponds there dry up), no evidence has as yet been found that the winter concentrations of Oahu result from the influx of birds from the other islands of the Hawaiian archipelago.

The North American coot is a migratory bird in the northern part of its breeding range, and ocean crossings up to 700 miles of distance are known (A.O.U. Check-list of North American Birds, Baltimore, 1957. p. 162). The existence of its Hawaiian subspecies is itself an evidence that coots were able to cross the Pacific between the North American continent and Hawaii. The slight taxonomic differences between the two forms indicate that this crossing happened relatively recently.

It could also be thought that subsequent influx of immigrant coots reinforced the genetic relationships (Cf. also Munro, G. C., Elepaio 3:37, 1943).

A theory of North American influx of coots lacks any evidence for the time being. It should be positively excluded as an explanation of winter concentrations until the more probable alternatives of habitat change or interisland migration have been thoroughly studied and documented.

Reprinted from PACIFIC SCIENCE, *vol. XIV, no. 4, October, 1960*

Marine Copepods of the Genus *Anthessius* from the Northeastern Pacific Ocean[1]

PAUL L. ILLG[2]

AMONG THE COPEPODS associated with invertebrates there is a remarkably homogeneous collection of species, predominantly associated with mollusks, comprising the genus *Anthessius* Della Valle 1880. The indications are strong that the mollusks will exclusively furnish the hosts of the members of the genus. Investigations of the invertebrate fauna of the Pacific Coast of the United States has resulted in the discovery of four species. One of these, *Anthessius navanacis* (Wilson, 1935), is known from California due to the fruitful ecological studies of Professor and Mrs. G. E. MacGinitie. From collections of the U. S. Steamer "Albatross," we have from Hawaii *Anthessius hawaiiensis* (Wilson, 1921). In the description of new species in a genus so anatomically consistent, it was necessary to invoke details not available in the original descriptions of these older species. Accordingly, they are redescribed below, with some emendations. For support of much of the research contributing to this paper I am indebted to Fund 171, State of Washington. The illustrations for three species are based on pencil renderings by Mr. R. U. Gooding. Other drawings and the writing of the paper have been completed during the tenure of a John Simon Guggenheim Memorial Foundation Fellowship. I am indebted to many colleagues for assistance in connection with this report, and am most particularly obliged to Mr. John E. Fitch for his considerable efforts in collecting for me the material of the species named for him below.

The genus *Anthessius* Della Valle dates from 1880, with two species described as associates of Mediterranean mollusks. A still earlier species is now included in the genus. This is *Boeckia arenicola* Brady 1872*a*, 1872*b*. As *Boeckia* is a preoccupied generic name, Brady subsequently referred to this species as *Lichomolgus arenicolus* (1880: 46–47). It has been referred to in this combination by several authors, and also as *Herrmannella arenicola,* following T. Scott (1898). No host was known for this species until Bocquet and Stock (1958) demonstrated that *A. arenicolus* is an associate of *Dosinia exoleta* (L), and, further, clarified the systematic confusion of this species with their *A. teissieri* 1958 in much of the published record. Such reinvestigations as that of Bocquet and Stock of many of the known species are needed to solve bionomic problems and to expand anatomical descriptions for provision of a sound basis for the resolution of the discrepancies found in the literature on the systematics of the genus. The work of these authors added to the revisionary summary of Monod and Dollfus (1932) and the review of Sewell (1949) provide the basis for the present treatment of the group. In the published record so far, the genus is still referred to the family Lichomolgidae, although the appropriateness of this attribution has already been questioned (Illg, 1949: 393). Myicolidae Yamaguti 1936 is available in Cyclopoida Poecilostoma among the families in the complex containing Clausidiidae and Lichomolgidae. I follow de Vos in Korringa and Lambert (1951: 18–19) in assigning *Lichomolgus spinosus* Raffaele e Monticelli 1885 not to *Anthessius,* but to the closely related genus, *Pseudomyicola* Yamaguti 1936. *Pseudomolgus* Sars 1916 is a synonym of *Anthessius* and the list of species so assigned must be transferred, as shown by Monod and Dollfus. The group of species now comprising *Anthessius* form a most coherent series of forms for which some morphological generalizations now can be made. Considerable emphasis has been laid by some authors on the importance of the condition of the segment of the first legs, relative to its alternative fusion with or separation from the cephalosome. Study of five species leads me to conclude that typically

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the cephalosome in the genus functionally includes the segment of the first legs. However, the legs themselves seem to function as part of the metasomal series of legs. The anterior part of the segment on the ventral side is involved in the formation of a posterior termination of the oral region. Functionally, then, the transition from cephalosome to metasome is strongly indicated as intrasegmental. In none of the species I have studied does the separation of the segment of the first legs from the anterior region seem to involve as free an articulation as that between successive pedigerous segments, although a well-developed inflected interruption of the integument may provide a conspicuous anterior boundary for the element. In the paratypic material of *A. navanacis* this feature was found to vary, one female being found with a well-developed suture indicating the segmental boundary, a second female showing no interruption of the integument.

The structure and ornamentation of the antennule emerge as remarkably consistent throughout the species and it is strongly probable that a basic form as well as a characteristic ornamentation will be found consistently when details have been presented for all species. A very interesting dichotomy exists with regard to sexual dimorphism in the armature of this appendage. Bocquet and Stock were the first to point out the remarkable complement of aesthetes in the antennule of males of *A. arenicolus* and *A. teissieri.* As can be seen by comparing their findings and the descriptions below, there is apparently a typical distribution of aesthetes on the antennules of females, these occurring regularly on segments 5, 6, and 7. Bocquet and Stock described in the males of the species they studied this same complement of aesthetes with additional aesthetes found on segments 2 and 4. Exactly the same pattern was found in the new species described below, *A. lighti.* However, on the basis of careful study of equally favorable material of *A. nortoni* and *A. fitchi,* both new species, I can say that no such dimorphism exists in these species. It will be of interest to see how this feature is found to be distributed among the species of the genus. Unfortunately the type material of *A. navanacis* available to me was not sufficiently well preserved to make possible determination of this feature, and for *A. hawaiiensis* I could not find males.

The antennae and the mandibles, maxillules, and maxillae are extremely similar throughout the species of the genus, so that a generic pattern might very soundly be said to exist, although there are minute details of specific variation. The maxillipeds, highly dimorphic in the sexes, are also somewhat more strongly specifically distinctive in details of ornamentation than are the other mouthparts. The swimming legs have a very consistent pattern of structure and ornamentation throughout the genus, with, however, fairly distinctive specific features of outline and proportion of segments and of fine details of minute ornamentation. Two major alternative patterns of armature appear through the series of species, some having three spines on the terminal segment of the fourth exopodite, some having four spines there. In all the species below in which I have been able to study both sexes (four of the five), I have found a sexual dimorphism of the first legs. On the terminal segment of the endopodite there is a spine and five setae in the female, two spines and four setae in the male. The species involved are sufficiently diverse in their other variable characteristics that I would venture to predict on the basis of these that such dimorphism will probably be found consistently throughout the genus.

The basic pattern of the fifth legs is consistent among the species, but there are distinctive variations in proportions and in the placement of the elements of the armature. There is a sexual dimorphism characteristically in this appendage, also, but the variation may be very subtle in degree in some species. Dimorphism of the caudal rami also seems substantially indicated, but for this feature additional investigation of the previously known species is required. Finally, with regard to sexual dimorphism it should be stated that in this group, where unusually large cyclopoid species are included, there is remarkably little difference in size of males and females in many of the species. More information is needed on this feature, but the situation is particularly striking in such a distinctive species as *A. fitchi,* described below, which is gigantic and equipped with strongly developed epimerae. The male is slightly larger than the female, which is unusual among poecilostome groups in general.

Reaching systematic conclusions in the genus *Anthessius* is difficult. The descriptions of many of the species are fragmentary or deal with details which are not readily comparable with those furnished in still other descriptions, so that the relatively subtly differentiated species become difficult to characterize as distinctive, although the information available convinces the taxonomic worker of the specific separation of the forms. Some characteristics which seem to serve for grouping species are discussed below. Finally a very rough key is presented to serve the function of demonstrating the specific separation of the new species described. As most of the features treated in the key are drawn from the literature, some of which is unsatisfactory for the details involved, it is to be regarded only as a synopsis, not as a reliable device for routine identification of species.

In general, the fifth leg of species is usually described and depicted with considerable detail and care. Grouping on the basis of this appendage should be fairly reliable. In *A. solecurti* Della Valle, the structure as figured and described is unique for the genus and readily serves to differentiate the species. Among the remaining species there are two general types of contour seen in the fifth leg of females. (The male of *A. investigatoris* Sewell 1949 has to be involved in this discussion, as the female of the species is not known.) In most species, the lateral margins of the free segment of the fifth leg are essentially parallel, although there may be some constriction at the base or toward the apex. In all, the appendage is narrow, so that the ratio of length to greatest width is much more than 3, ranging from about 3.2 to 4.5 or more. In the fifth leg of the remaining species the free segment is much broader and more platelike. The margins tend to expand and the armature may be concentrated on or near a broad distal margin. In such forms the ratio of length to width of the free segment is much less than 3, ranging from about 1.8 to 2.7, as discernible from figures accompanying descriptions in most cases. *A. navanacis* (Wilson), which is assignable to this group, is also readily separated from all members of the genus by the distinctive outline of the fifth leg, with marked basal constriction. Few anatomical details are available for *A. pleurobrancheae* Della Valle, but in the description the structure of the fifth leg is stressed, and this species is unique among those falling into the category just described by completely lacking marginal ornamentation of spinules on the free segment. As remarked above a useful dichotomy exists with regards to the armature of the fourth swimming legs, but this detail is not available from all species descriptions. Finally, there are readily determinable groupings available based on the ratio of length to width of caudal rami, and in most descriptions information on this feature or fairly good illustration is provided. The degree of variability of this character in any given species remains to be determined.

KEY TO SPECIES OF *Anthessius*

Based on adult females, but including *A. investigatoris* Sewell 1949 on the basis of the male. *A. pleurobrancheae* Della Valle 1880 has been included, after the treatment of Stock (1959), although the original description was very scanty and Claus' account (1889) does not extensively supplement Della Valle's. Species recently described (Humes, 1959; Stock, 1959) have been included in the key, but were not treated in the discussions in this paper.

1a. Body habitus very modified, cephalosome much expanded in outline, thoracic segments with widely extending epimera, caudal rami elongate, laminate............................***fitchi,*** new species

1b. Body in general approaching typical cyclopoid habitus 2

2a. Ratio of length to width of terminal segment of fifth leg more than 3........ 3

2b. Ratio of length to width of terminal segment of fifth leg less than 3..........12

3a. Terminal segment of exopodite of fourth leg with 4 spines...................... 4

3b. Terminal segment of exopodite of fourth leg with 3 spines..................... 9

4a. Ratio of length to width of caudal ramus about 1........*brevifurca* Sewell 1949

4b. Ratio of length to width of caudal ramus much more than 1......................... 5

5a. Maxilla bearing more than 10 external marginal teeth.......... *pleurobrancheae* Della Valle 1880
5b. Maxilla bearing at most 6 external marginal teeth 6
6a. Ratio of length to width of caudal ramus about 2.6.......... ***lighti*, new species**
6b. Ratio of length to width of caudal ramus about 4.......... 7
7a. Interior margin of fifth leg bearing distal group of slender spinules at distal third and a group of slender spinules in the middle of the segment.......... *arenicolus* (Brady 1878)
7b. Interior margin of fifth leg bearing, with exception of distal group of slender spinules at distal third, no spinules or setae 8
8a. Ventral surface of last segment of urosome with 2 prominent rows of strong spinules.......... *solecurti* Della Valle 1880
8b. Ventral surface of last segment of urosome with 2 rows of hardly discernible spinules.......... *teissieri* Bocquet and Stock 1958
9a. Ratio of length to width of caudal ramus about 1.5.......... *investigatoris* Sewell 1949
9b. Ratio of length to width of caudal ramus much more than 1.5..........10
10a. Ratio of length to width of caudal ramus about 3.......... ***nortoni*, new species**
10b. Ratio of length to width of caudal ramus more than 3.5..........11
11a. Terminal segment of antenna at least twice as long as wide.......... *leptostylis* (Sars 1916)
11b. Terminal segment of antenna about 1.5 times as long as wide.......... *dilatatus* (Sars 1918)
12a. Terminal segment of fourth exopodite with 4 spines..........13
12b. Terminal segment of fourth exopodite with 3 spines..........16
13a. Maxilla with low apical sclerotized portion, not inclining anteriorly in marked angle to remainder of appendage.......... *hawaiiensis* (Wilson 1923)
13b. Maxilla with apical portion erect, large, sharply angled 14
14a. Exterior margin of fifth leg without spinules or setae.......... *groenlandicus* (Hansen 1921)
14b. Exterior margin of fifth leg with row of spinules or setae..........15
15a. Exterior margin of fifth leg bearing only about 5 short, stout, conical spinules.......... *minor* Stock 1959
15b. Exterior margin of fifth leg bearing many long, slender spinules or setules.......... *concinnus* (A. Scott 1909)
16a. Second and fourth segments of antennule extremely elongate, over 4 times as long as wide .... *navanacis* (Wilson 1935)
16b. Second and fourth segments of antennule of moderate proportions, less than 3 times as long as wide.......... *pinnae* Humes 1959

The literature contains references to species of *Anthessius* which have not yet received formal systematic characterization: *Pseudomolgus* sp. Wilson (1921: 15); *Pseudomolgus* sp. Wilson (1923: 4); and *Anthessius* sp. Humes and Cressey (1958: 935).

Anthessius Della Valle 1880

Boeckia Brady 1872*a*; Brady 1872*b*.
Lichomolgus Brady 1880 (pars); auctorum.
Anthessius Della Valle 1880; Canu 1891; Monod and Dollfus 1932; auctorum.
Hermanella Thompson and Scott 1903 (pars); auctorum.
Pseudomolgus Sars 1916; auctorum.

The complete synonymy of the genus is not given here, although the basis for tracing all references is provided in the above and the bibliographies provided in the references cited. There are several systematic problems connected with the genus still to be clarified.

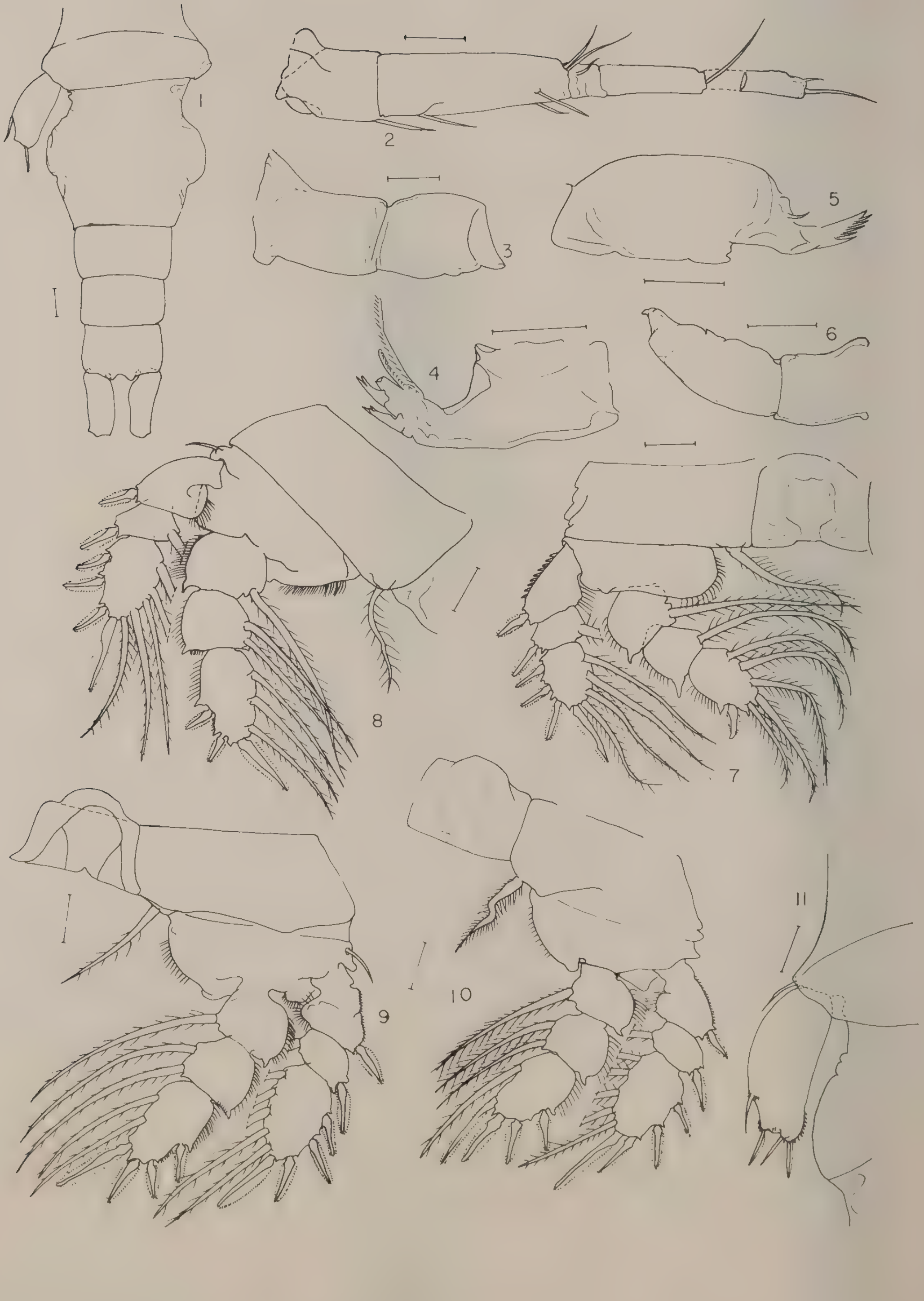
In many regards the diagnosis of the genus provided by Della Valle still holds, although some of his characters were erroneous. However the modern definition may well be based on the original description. The body is mostly cyclopoid, but some considerable elaboration of body processes may occur. The segment of the first legs is functionally involved with the cephalosome in part and may be entirely anatomically fused. The antennule is 7-segmented. The antenna is 3-segmented, the basal 2 segments each with 1 seta, the terminal segment with several setae and several characteristic articulated hooks. The mandible is an unsegmented flat plate tapering apically in a long setiform process. An equally well-developed accessory process is articulated on the anterior margin just proximal to the distal lash. Marginal ornamentation is strongly developed in both elements. The maxillule is a flat plate, with expanded and somewhat incised apical margin, with armature consisting of an articulated spine and seta. The maxilla has a greatly expanded basal segment, the flat apical segment tapering and bending anteriorly to form a heavily cuticularized element with right-angled outline, usually with 1 accessory articulated spine or seta, and with the margin developed as a series of conspicuous spinous processes. The maxilliped of the female is obscurely 3-segmented, with reduced armature. In the male the maxilliped is 3-segmented, the terminal 2 segments participating in a characteristic subchela. Hand of subchela inflated and with ornamentation of spinules and spines. Finger of subchela very elongate and bearing accessory seta. Legs 1 to 4 biramous, all rami trimerous. Armature well developed, the most characteristic pattern being that of the terminal segments of the third endopodite, bearing 4 spines and 2 setae; that of the terminal 2 segments of the fourth endopodite, bearing on segment two 2 setae, on three 1 seta and 4 spines; and that of the terminal segment of the fourth exopodite, this bearing 5 setae and alternatively 3 or 4 spines. The fifth leg has 1 free segment, the basal element being only a setiferous prominence of the body segment. The flat, elongate free segment bears four elements of armature, characteristically 3 spines and a seta. The sixth legs are not particularly distinctive among those of poecilostomes, and the caudal rami are variable in proportions, although the typical cyclopoid armature is consistently well developed.

Sars designated *Boeckia arenicola* Brady as the type of *Pseudomolgus.* The type for *Anthessius* has not yet been fixed, but must be selected from one of the two original species of Della Valle, *A. pleurobrancheae* and *A. solecurti.* On the basis of the redescription and extensive illustration of *A. solecurti* by Stock (1959), this species is herewith designated as the type of the genus.

Anthessius hawaiiensis (Wilson)
Figs. 1–11

Pseudomolgus hawaiiensis C. B. Wilson 1921. Type locality off South Coast of Molokai, Hawaiian Islands, "Albatross" Station 3853, type host *Pleurobranchus* sp.

SPECIMENS EXAMINED: Wilson's types were seen in the U. S. National Museum and were found to compare reasonably well with the habit figures he presented, although none were in good condition. A female paratype, USNM 53565, was dissected, and although some of the appendages were lost in preservation and some in dissection of the fragile specimen, a description was prepared to provide details for comparison with the species described below. Wilson used a different terminology for mouthparts from that now current, so his statements about the first maxilla refer to our mandible, his palp of first maxilla is our maxillule, but his second maxilla corresponds to our usage. His description in general corresponds to the type specimens, but his illustrations are variable in reliability. The antennule and antenna are very generally depicted, without providing details of armature. The mandible is generally illustrated, although some details of the armature are lacking. The maxillule is inadequately depicted. The maxilla is presented in essential outline, but the detailing is somewhat misleading. He indicates more processes on the terminal segment than the type material corroborates. For the female, the first leg is essentially depicted, although the figure does not indicate completely the apical spine of the terminal segment of the exopodite. The second and third legs are illustrated in essential rough outline. The illustration of the fourth leg presents serious discrepancy from that for the male and from the type material. The exopodite is not depicted as possessing on the terminal segment the 3 lateral and 1 terminal spines illustrated for the male and which I find on the paratypic female. The figure of the endopodite corresponds in rough essentials. The illustration of the fifth leg cor-



responds in rough essentials to the paratype, but the armature was incompletely represented. For the male, the third leg was represented as corresponding in rough essentials to the female, the fourth leg was illustrated so that the exopodite corresponds to what I found in the female paratype and serves to indicate a correction can be made in the illustration for the female. However the illustration of the endopodite does not represent the condition found in any *Anthessius* male I know of. This figure then is subject to question. The figures 55, 56, representing the fifth leg of the male, do not agree. I was unable to reinvestigate the appendage.

DESCRIPTION: Female (Figs. 1–11), body length 4 mm., greatest width 2 mm., based on Wilson's original description. Body of rather generalized cyclopoid contours, but with most thoracic and abdominal segments distinct, so that regionalization is not emphatic. Cephalosome a fused complex bearing appendages through first swimming legs and comprising .34 of total body length, measured from apex of cephalosome to end of a caudal ramus. Segment of first legs not free, but strongly indicated by lateral indentations and surface grooves. Metasome including segments of second through fourth legs, with general body articulation between segments of legs 4 and 5. Urosome (Fig. 1) a complex including segment of legs 5, genital segment and 3 additional abdominal segments, considering element bearing anal opening and supporting caudal rami as terminal segment. Urosome comprising .41 of total body length. Genital segment expanded laterally.

Antennule (Fig. 2) essentially 7-segmented, but with complicated articulation and integumental modification between second and third segments, so as to suggest either coalescence or incipient separation of an additional minute segment. Approximate proportional lengths of segments, basal to distal: Segment I, 3; II, 6; III, 1; IV, 3.5; V, 2; VI, 1; VII, 1. Setae varying in length; count per segment indeterminable in available material.

Antenna (Fig. 3) with segmental composition much obscured by additional flexures, involving integumental folds, and torsions of one region of appendage on adjoining regions, but probably essentially 3-segmented. Basal segment clear-cut, apical articulation transverse, no armature determinable. Second segment with very complicated distal articulation, this proceeding diagonally across appendage; no armature determinable. Terminal segment with cuticularized ridges and folds and with very broad distal margin furnishing insertion for elaborately articulated clawlike elements and setae. Details of armature indeterminable from available material.

Mandible (Fig. 4) a flat plate, with very cuticularized anterior and posterior margins. Appendage terminating in long lashlike blade with complicated marginal ornamentation. Two most basal elements of ornamentation flat toothlike structures, compound apically and articulating with margin of appendage. Remainder of ornamentation a long row of graduated denticles. On anterior margin articulated a long lashlike auxiliary seta with conspicuous graduated row of cilia on outer margin. Between apical lash and auxiliary seta an articulated cuticular piece with some marginal ornamentation.

Maxilla (Fig. 5) with very long articulation with body surface, resulting in characteristic massive basal segment, on which articulates flattened apical segment with heavy cuticularization. Apex produced in sharp angle anteriorly with toothlike expansions of cuticle forming a medial saw-edge. Five marginal teeth, formed by flangelike protrusions of cuticle. Apex produced as short spinelike process. Inserted at base of angle of curvature of this segment and lying on its surface an articulated setule.

Maxilliped (Fig. 6) fairly long, 2-segmented. Basal segment a little over half as long as distal. Terminal segment with apical spinelike process. Margins somewhat cuticularized.

First legs (Fig. 7) with well-developed bimerous protopodites, yoked by substantial inter-

FIGS. 1–11: *Anthessius hawaiiensis* (Wilson). The scales accompanying certain figures represent 0.1 mm. Female: 1, urosome; 2, antennule; 3, base of antenna; 4, mandible (partial); 5, maxilla; 6, maxilliped; 7, first leg; 8, second leg; 9, third leg; 10, fourth leg; 11, fifth leg.

coxal plate. Basal width of basipodite less than width of distal margin of coxopodite, so medial seta of coxopodite inserted on free portion of margin. Coxopodite seta very long, extending rather more medially than distally, its length slightly greater than width of intercoxal plate. Basipodite with row of cilia on curving medial margin. Armature of trimerous exopodite: first segment, 1 lateral spine; second segment, 1 lateral spine, 1 medial seta; third segment, 3 lateral spines, 1 terminal spine, 1 terminal seta, 3 medial setae. First segment with fine spinules on lateral margin and row of cilia on medial margin. Proximal 5 spines of ramus each outlined with serrate hyaline flange. Apical spine with external hyaline flange and entire inner margin. Endopodite flexed medially and proximally. Armature: first segment, 1 medial seta; second segment, 1 medial seta; third segment, 1 lateral spine, set in distinct emargination, 2 apical setae, 3 medial setae. Each of 2 basal segments produced at distal lateral corner as spinous cuticular process. Spine of terminal segment subtended by such process, and with outlining hyaline flange. Every segment with row of cilia on lateral margin. Setae of coxopodite and rami with plumose ciliation.

Second legs (Fig. 8) with well-developed bimerous protopodites yoked by substantial intercoxal plate. Medial seta of coxopodite on medial free portion of border of segment. Seta about as long as width of intercoxal plate. Basipodite with tiny lateral seta; medial margin with dense row of cilia. Exopodite trimerous. Armature: first segment, 1 lateral spine; second segment, 1 lateral spine, 1 medial seta; third segment, 3 lateral spines, 1 terminal spine, 1 terminal seta, 4 medial setae. First segment with row of fine spinules on lateral margin, cilia on medial margin. Proximal 5 spines of ramus each outlined with serrate, hyaline flange. Apical spine with external hyaline flange and very small internal flange. Endopodite flexed medially and proximally. Armature: first segment, 1 medial seta; second segment, 2 medial setae; third segment, 2 lateral spines, set in steplike emarginations, 1 terminal spine, 3 medial setae. Each of 2 basal segments produced at distal lateral corner as spinous cuticular process. Spines of terminal segment subtended by such processes, but these somewhat less developed than those of basal segments. Spines of terminal segment with hyaline flanges. Each segment with row of cilia on lateral margin. Setae of coxopodite and rami with plumose ciliation.

Third legs (Fig. 9) with well-developed bimerous protopodites yoked by substantial intercoxal plate. Medial seta of coxopodite, about equal to width of intercoxal plate, inserted on medial free portion of distal border of segment. Basipodite with small lateral seta; medial margin with row of cilia. Exopodite, extended almost directly, without notable flexure, trimerous. Armature: first segment, 1 lateral spine; second segment, 1 lateral spine, 1 medial seta; third segment, 3 lateral spines, 1 terminal spine, 1 terminal seta, 4 medial setae. First segment with row of fine spinules on lateral margin, dense row of cilia on medial margin. Proximal 5 spines of ramus each outlined with serrate, hyaline flange. Apical spine with external hyaline flange and internal margin entire. Trimerous endopodite flexed medially and proximally. Armature: first segment, 1 medial seta; second segment, 2 medial setae; third segment, 2 lateral spines, set in steplike emarginations, 2 terminal spines, 2 medial setae. Each of 2 basal segments produced at distal lateral corners as small spinous cuticular processes. Spines of terminal segment subtended by such processes, but these even less developed than those of basal segments. Each segment with dense row of cilia on lateral margin. Spines of terminal segment with hyaline flanges. Setae of coxopodite and rami with plumose ciliation.

Fourth legs (Fig. 10) with well-developed bimerous protopodites yoked by substantial intercoxal plate. Medial seta of coxopodite inserted on medial free portion of distal border of segment; length about equalling width of intercoxal plate. Medial margin of basipodite with short row of cilia. Exopodite, extended with slight flexure, trimerous. Armature: first segment, 1 lateral spine; second segment, 1 lateral spine, 1 medial seta; third segment, 3 lateral spines, 1 terminal spine, 1 terminal seta, 4 medial setae. First segment with row of fine spinules on lateral margin, cilia on medial margin. Proximal 5 spines of ramus each outlined with serrate, hyaline flange. Apical spine with external hyaline flange and internal margin entire. Trimerous endopodite with slight flexure. Armature: first segment, 1 medial seta; second segment, 2 medial setae; third segment, 2 lateral spines set in steplike emarginations, 2 apical spines, 1 medial seta. Medial setae of all segments reduced somewhat in length. Each of basal 2 segments produced slightly at distal lateral corner as small spinous cuticular process. Most proximal spine of terminal segment subtended by such process, and another apical on segment. Each segment with dense row of cilia on lateral margin. Spines of terminal segment with hyaline flanges. Setae of coxopodite and rami with plumose ciliation.

Fifth legs (Fig. 11) with probably 2 segments represented, basal consisting only of expansion on body posteriorly and laterally to furnish articulation of distal segment, and with a small seta laterally, representing armature. Second segment broad, flattened with cuticularized medial and lateral margins. Length about 2.5 times greatest width. Armature 2 spines and 2 setae, spaced on lateral and terminal margins: 1 lateral seta at about distal .8 of lateral margin; 1 spine at lateral distal corner; 1 seta near medial distal corner; 1 apical spine at medial distal corner. Spines subtended by small groups of spinules, these continuing as short row on distal fifth of medial margin.

Caudal ramus about 2.5 times as long as greatest width and 1.15 times as long as anal segment. Setal armature not determinable from available material.

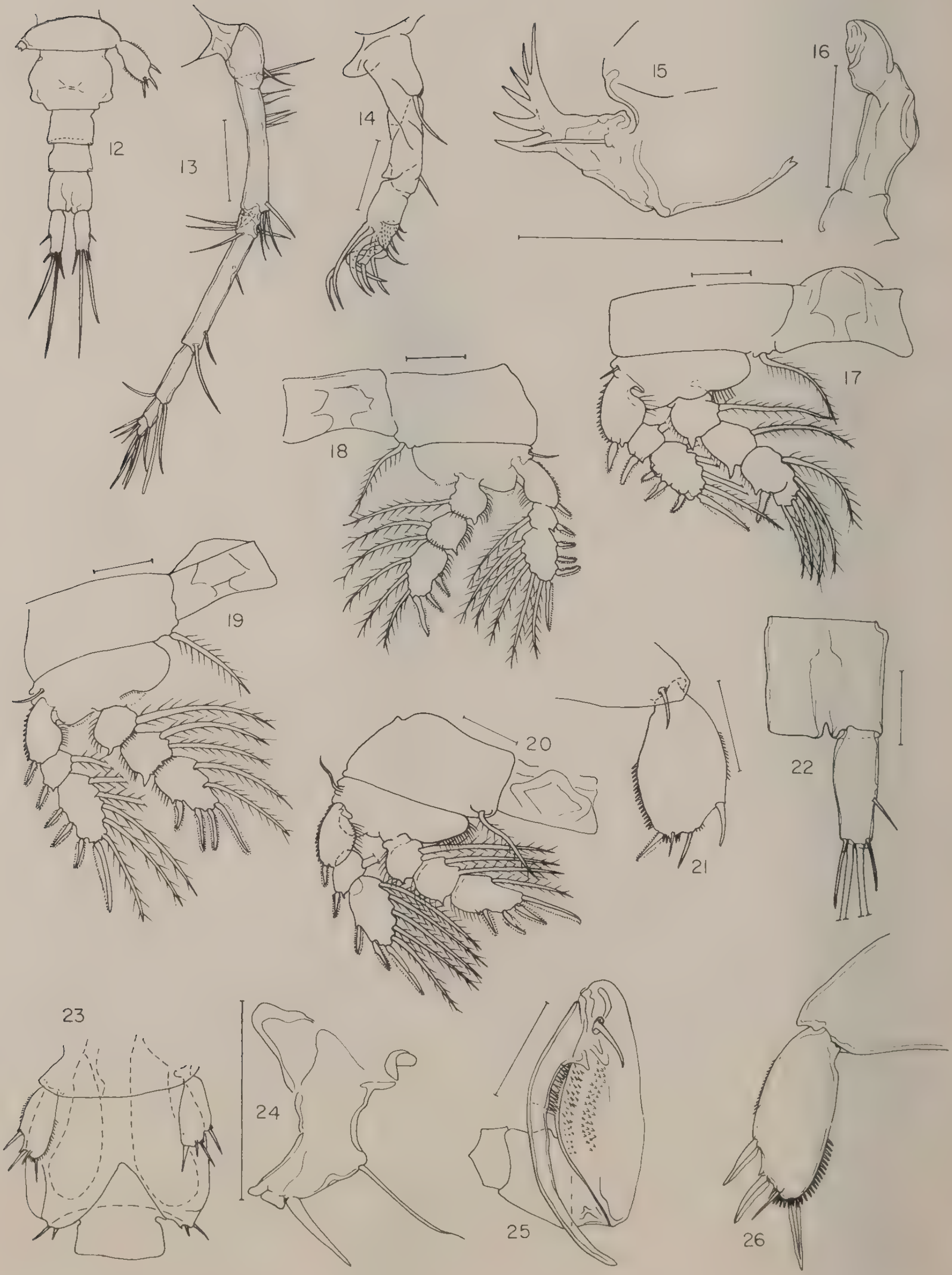
REMARKS: Due to the small amount of type material the male of this species could not be reinvestigated. According to the original description by Wilson the length of the male is 2.85 mm., the width 1.25 mm., and the usual features of anatomical dimorphism appear to occur. Attempts have been made to re-collect this species. The host, as indicated by the original description, quite possibly is a fairly common form in Hawaiian waters, but no further records of the copepod have come to light.

The species is differentiated from others of the genus in the key above. Many details of the anatomy should be reinvestigated when well-preserved specimens become available. The species is one of the larger ones known for the genus.

Anthessius navanacis (Wilson)
Figs. 12–26

Pseudomolgus navanacis, C. B. Wilson, 1935. Type locality, Laguna Beach, California, *Navanax inermis* (Cooper), type host.

SPECIMENS EXAMINED: Wilson's types were seen in the U. S. National Museum, and were found to compare reasonably well with the habit figures he presented (but see below, under body form). Two female paratypes and two male paratypes, one pair each from USNM 54082 and USNM 64062, were dissected to compare with the original description. The specimens showed some variation in body segmentation and in the strength of development of the spines of the swimming legs, but these were of minor grade. The specimens in some details in which they agree with each other do not correspond to some details of the original description and accompanying illustrations. Accordingly, the species is redescribed below, with details added for purposes of comparison with other species treated in the present study. Wilson was using a different terminology for mouthparts from that now current, so his statements about the first maxilla refer to our mandible. His description and figure for this appendage are in good agreement with generalities about *Anthessius* species, and, as I was unable to dissect out in good condition the mandible from the paratypes I examined, I can add no further information. Some important discrepancies in the descriptions and illustrations for other appendages in the original description should be noted. The armature described for the second antenna, 6 or 7 stout claws and 1 or 2 setae, does not correspond with the 4 claws and 7 setae described below. For the 4 pairs of swimming legs, a misinterpretation of the cuticular specializations of some segments led to presentation in the original description of an armature which does not correspond with any known for a species of *Anthessius*. The exopodites are adequately described and illustrated. For the endopodites, spinous processes were counted as spines and some other discrepancies from the condition in the para-



types occur. The illustration and description of the fifth leg in the female corresponds in rough essentials to the condition in the paratype, but one element of the armature was omitted. For the male, the maxilliped was described and figured in approximate correspondence with that of the paratypes, but Wilson overlooked a well-developed basal segment, so that the appendage was referred to as 2-segmented.

DESCRIPTION: Female (Figs. 12–22): Body length 2.0 mm., greatest width 1.40 mm., based on Wilson's original description. Body of rather generalized cyclopoid contours, but with metasomal and abdominal segments distinct, so that posterior regionalization is not emphatic. Cephalosome a fused complex bearing appendages through first swimming legs and comprising .4 of total body length, measured from apex of cephalosome to end of a caudal ramus. Original description stated that segment of the first legs is fused with the cephalothorax and indicated so as an antomical segment by slight marginal indentations. Paratypes (topotypic) from Laguna Beach (USNM 54082) showed the segment so clearly delimited as almost to justify considering it a free element. Paratypes from Anaheim Slough, California (USNM 64062) show fusion as in the original description.

Antennule (Fig. 13) essentially 7-segmented, but with complicated articulation and integumental modification between second and third segments, so as to suggest either coalescence or incipient separation of an additional minute segment, which if present would raise number to 8. Approximate proportional lengths of segments, basal to distal: Segment I, 3; II, 6.5; III, 1.5; IV, 6; V, 3; VI, 1.5; VII, 1. Setae varying in length, count per segment undeterminable due to poor preservation of available specimens.

Antenna (Fig. 14) with segmental composition much obscured by additional flexures, involving integumental folds, and torsions of one region of appendage on adjoining regions, probably essentially 3-segmented. Basal segment without clear-cut, apical articulation, bearing 1 short external seta. Second segment with very complicated distal articulation, this proceeding diagonally across appendage; 1 short seta distally and externally inserted. Terminal segment with cuticularized ridges and folds and with very broad distal margin furnishing insertion for 4 elaborately articulated clawlike elements and 2 setae. Another seta near distal margin. A subapical group of 4 setae of diverse lengths. Total elements—4 claws, 7 setae.

Mandible a flat plate, with cuticularized anterior and posterior margins. Appendage terminating in long lashlike blade with complicated marginal ornamentation. Two most basal elements of ornamentation flat structures compound apically and articulating with margin of appendage. Remainder of ornamentation a row of graduated denticles. On anterior margin of mandible articulated a long lashlike auxiliary seta with conspicuous marginal ornamentation.

Maxillule of characteristic type for genus, an elongate lobe with flaring apex. On apex a more medial spine and far lateral seta. More detailed description presented for male, below.

Maxilla (Fig. 15) with very long articulation with body. Characteristic massive basal segment, on which articulating flattened apical segment, with heavy cuticularization. Apex produced in sharp angle anteriorly, with toothlike expansions of cuticle forming medial saw-edge. Five large teeth formed by flangelike protrusions of cuticle. Apex produced as more elongate spinelike process, to total number of outgrowths 6. In some specimens there may be 1 more or 1 less tooth. Inserted at base of angle of curvature of distal segment, and lying on surface, an articulated, fairly long seta.

Maxilliped (Fig. 16) a prominent mouthpart, as seen in general habitus of mouth area, but with little development of segmentation or ornamentation. Three segments suggested by folds and flexures of integument. Terminal portion with folds and indentations of cuticularized surface, but with no elements of armature.

First legs (Fig. 17) with well-developed

FIGS. 12–26: *Anthessius navanacis* (Wilson). The scales accompanying certain figures represent 0.1 mm. Female: 12, urosome; 13, antennule; 14, antenna; 15, maxilla; 16, maxilliped; 17, first leg; 18, second leg; 19, third leg; 20, fourth leg; 21, fifth leg; 22, anal segment and caudal ramus. Male: 23, segments of fifth and sixth legs; 24, maxillule; 25, maxilliped; 26, fifth leg.

bimerous protopodites, yoked by substantial intercoxal plate. Basal width of basipodite less than width of distal margin of coxopodite, so medial seta of coxopodite inserted on free portion of margin. Coxopodite seta relatively long, extending rather more medially than distally, and with its length slightly less than the width of intercoxal plate. Basipodite with small lateral seta proximal to insertion of exopodite and with row of stout cilia on curving medial margin. Exopodite held at angle to protopodite, trimerous. Armature: first segment, 1 lateral spine; second segment, 1 lateral spine, 1 medial seta; third segment, 3 lateral spines, 1 terminal spine, 1 terminal seta, 3 medial setae. First segment with fine spinules on lateral margin, row of cilia on medial margin. Proximal 5 spines of ramus each outlined with serrate hyaline flange. Apical spine with external hyaline flange and internal row of cilia. Endopodite flexed medially and proximally. Armature: first segment, 1 medial seta; second segment, 1 medial seta; third segment, 1 lateral spine, set in distinct emargination, 2 apical setae, 3 medial setae. Each of 2 basal segments produced at distal lateral corner as strong spinous cuticular process. Spine of terminal segment subtended by such process, and with outlining hyaline flange. Each segment with row of cilia on lateral margin. All setae of leg with plumose ciliation.

Second legs (Fig. 18) with well-developed bimerous protopodites yoked by substantial intercoxal plate. Medial seta of coxopodite on medial free portion of border of segment. Seta about as long as width of intercoxal plate. Basipodite with small lateral seta; medial margin with cilia. Exopodite trimerous. Armature: first segment, 1 lateral spine; second segment, 1 lateral spine, 1 medial seta; third segment, 3 lateral spines, 1 terminal spine, 1 terminal seta, 4 medial setae. First segment with row of spinules on lateral margin, cilia on medial margin. Proximal 5 spines of ramus each outlined with serrate, hyaline flange. Apical spine with external hyaline flange and internal margin entire. Endopodite slightly flexed medially and proximally. Armature: first segment, 1 medial seta; second segment, 2 medial setae; third segment, 2 lateral spines, set in steplike emarginations, 1 terminal spine, 3 medial setae. Each of basal 2 segments produced at distal lateral corner as small spinous cuticular process. Proximal spine of terminal segment also subtended by such process. Each segment with row of cilia on lateral margin. Spines of terminal segment with hyaline flanges. All setae of leg with plumose ciliation.

Third legs (Fig. 19) with well-developed bimerous protopodites yoked by substantial intercoxal plate. Medial seta of coxopodite about as long as width of plate, inserted on medial free portion of distal border of segment. Basipodite with small lateral seta; medial margin with cilia. Exopodite, extended directly, without notable flexure, trimerous. Armature: first segment, 1 lateral spine; second segment, 1 lateral spine, 1 medial seta; third segment, 3 lateral spines, 1 terminal spine, 1 terminal seta, 4 medial setae. First segment with row of spinules on lateral margin, row of cilia on medial margin. Proximal 5 spines of ramus each outlined with serrate, hyaline flange. Apical spine with external hyaline flange and internal margin entire. Trimerous endopodite slightly flexed medially and proximally. Armature: first segment, 1 medial seta; second segment, 2 medial setae; third segment, 3 lateral spines, set in steplike emarginations, 1 terminal spine, 2 medial setae. Each of 2 basal segments produced at distal lateral corner as moderately long spinous cuticular process. Proximal spine of terminal segment subtended by such process, but this less developed than those of basal segments. Each segment with row of cilia on lateral margin. Spines of terminal segment with hyaline flanges. All setae of leg with plumose ciliation.

Fourth legs (Fig. 20) with well-developed bimerous protopodites yoked by substantial intercoxal plate. Medial seta of coxopodite inserted on medial free portion of distal border of segment. Basipodite with small lateral seta; medial margin with row of cilia. Exopodite, with somewhat medial flexure, trimerous. Armature: first segment, 1 lateral spine; second segment, 1 lateral spine, 1 medial seta; third segment, 2 lateral spines, 1 terminal spine, 1 terminal seta, 4 medial setae. First segment with row of fine spinules on lateral margin, cilia on medial margin. Proximal 4 spines of ramus each outlined with serrate, hyaline flange. Apical spine with external hyaline flange and internal margin, except for slight notch, entire. Trimerous endopodite with medial flexure. Armature: first segment, 1 medial seta; second segment, 2 medial setae; third segment, 3 lateral spines set in steplike emarginations, 1 terminal spine, 1 medial seta. Medial setae of distal segment very short. Each of basal 2 segments produced at distal lateral corner as small spinous cuticular process. Basal spine of terminal segment also subtended by such process. Each segment with row of cilia on lateral margin. Spines of terminal segment with hyaline flanges, complete in lateral spines, only on lateral margin of terminal spine. All setae of leg with plumose ciliation.

Fifth legs (Fig. 21) with probably 2 segments represented, basal consisting only of expansion on body segment posteriorly and laterally to furnish articulation of distal segment, with 1 small seta representing armature. Second segment elongate, flattened, with cuticularized medial and lateral margins. Length about 1.8 times greatest width. Armature 3 spines and 1 seta, spines about equally spaced on lateral and terminal margins: 1 lateral spine at distal corner of lateral margin; 1 spine at about midpoint of broad apical margin; 1 spine at medial distal corner; 1 seta near medial distal spine. Seta and apical spine subtended by small groups of spinules. Spinules also forming short rows on distal half of medial margin and middle third of lateral margin.

Sixth legs probably represented by small setiferous knob in depression at aperture of oviduct, located dorsally on lateral expansion of genital segment. Two subequal setules forming armature.

Caudal ramus (Fig. 22) about 2.5 times as long as greatest width and about as long as anal segment. Armature 6 setae. Of apical quartet of setae, medial of central 2 longest, about 4 times as long as ramus; adjacent long seta 2 times length of ramus. Medial apical seta about .6 as long as ramus; lateral apical seta about .4 as long as ramus. Lateral marginal seta short, about .4 as long as ramus, inserted on lateral margin at about distal third. Dorsal medial seta very short, inserted just subapically.

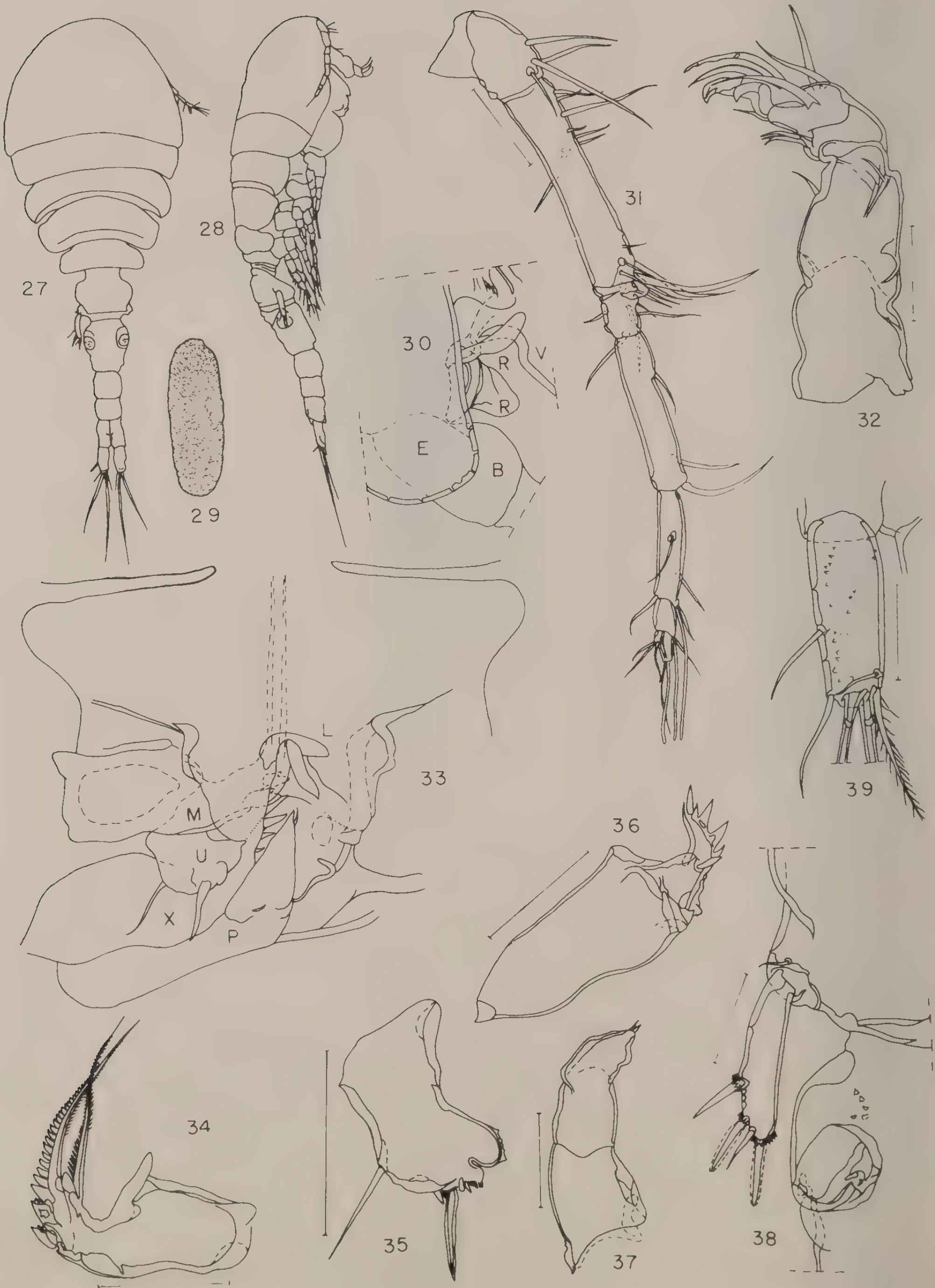
MALE (Figs. 23–26): Body length 1.5 mm., greatest width .5 mm., based on Wilson's original description. Body very generalized cyclopoid in type. Cephalosome bearing first legs, its segment indicated by slight marginal indentations. Metasome of free segments of legs 2 to 4. Urosome of free segments of legs 5, 6, and 4 abdominal segments, including segment bearing anus and caudal rami. Segments of legs 5 and 6 much coalesced in a genital complex (Fig. 23) accommodating spermatophores which are very elongate.

Antennules, antennae and mouthparts, except maxilliped, as in female. Maxillule (Fig. 24) of characteristic type of the genus; elongate, with shoe-shaped apex. A long medial seta and subapical spine. Two subequal small apical lobes.

Maxilliped (Fig. 25) highly dimorphic, developed as massive, complicated appendage, probably trimerous. In mouth area, maxillipeds held in characteristic posture, tending to align along longitudinal axis of body, second segment moving in sagittal plane over first segment, and terminal segment tending to swing in frontal plane. First segment about one-third length of second, unornamented. Second segment tapered apically, margin medial in position in normal posture of appendage bearing characteristic ornamentation, serving to act in conjunction with clawlike terminal segment in prehensile function. Medial ornamentation consisting of 2 longitudinal multiple rows of denticles, and a single row of long spinules. In addition, near midpoint of medial margin a short, stout spine. Terminal segment forming very complicated region of articulation on apex of second segment, prolonged as curving claw, longer than second segment. One seta inserted on expanded region of articulation.

Dimorphism also expressed particularly in first legs, remaining swimming legs very similar to those of female. Protopodites and exopodites of first legs essentially as in female. Basal segments of endopodites as in female, terminal segment of each with lateral spine, 1 apical spine, 1 apical seta, 3 medial setae, apical spine representing a seta of female appendage.

Fifth leg (Fig. 26) not greatly like that of female in outline, but with similar ornamentation. Length about 2.5 times greatest width, thus a much narrower appendage, without con-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spicuous basal constriction. Medial row of spinules more extensive, reaching apex.

Sixth legs (Fig. 23) ventrolateral on genital segment, involved in very complicated manner with structure of reproductive opening. Most obviously representative of appendage a small prominence bearing 2 setae, the more medial about half as long as lateral.

REMARKS: The species seems to belong to a southern California fauna, as it was collected from at least two localities, Anaheim Slough and Laguna Beach, by the MacGinities. In considerable exploration and study of marine zoology on the West Coast no collections from further north have yet come to my attention, although the host is recorded as ranging very widely on the coast of California and has been closely observed frequently. Details of the antennules should be reinvestigated on freshly collected specimens.

Anthessius lighti, new species

Figs. 27–58

TYPES: Holotypic female, USNM 103307, allotypic male, USNM 103308, paratypes, USNM 103309; additional paratypes in Alan Hancock Foundation, University of Southern California, and in author's collection. Type locality, Bodega Bay, California, from *Aplysia californica* Cooper.

SPECIMENS EXAMINED: Several lots of this species are included in the material studied, but as far as can be determined they represent a single collection from *A. californica,* from Bodega Bay, California, June 1, 1941, O. Hartman and E. C. Dougherty, many specimens, males and females. The descriptions below and the illustrations are based on a number of specimens, some unmounted, some whole mounts, some temporarily mounted dissections, some permanently mounted dissections. Two of the latter have been selected as holotype and allotype.

DESCRIPTION: Female (Figs. 27–43): Body length 2.67 mm., greatest width 1.14 mm., averages for 10 specimens. Body (Figs. 27, 28) of rather generalized cyclopoid contours, but with most thoracic and abdominal segments distinct, so that regionalization is not emphatic. Cephalosome a complex bearing appendages through first swimming legs and comprising .33 of total body length measured from apex of cephalosome to end of a caudal ramus. General contour and internal structure strongly indicating segment of leg 1 a part of cephalosome, but this segment clearly demarcated dorsally and anteriorly by continuous articulationlike groove and well-developed marginal indentations. Ventrally segment of leg 1 apparently contributing to cephalosome in forming massive midventral bulge between mouthparts and leg 1. First legs situated on posterior edge of segment, directed posteriorly, obviously behaving functionally as part of metasomal group of legs. On anterior margin apex of head protruded in a slight bulge between bases of widely separated antennules. No rostrum, apical ventral region of head a wide flattened expanse between bases of antennules and antennae. Metasome including pedigerous segments of second through fourth legs, with general body articulation between segments of legs 4 and 5. Segment of fourth legs with distinctive bilateral, ventral structures. Fourth legs borne on anterior end of ventral surface of segment. At each side on posterior region of ventral surface two subequal lobes extending posteriorly. Lobes visible in dorsal view (Fig. 30) of intact animal, as lying between segments of legs 4 and 5 and medial to the fourth legs. Urosome a complex including segment of legs 5, a genital segment and 3 additional abdominal segments, considering element bearing anus and supporting caudal rami as terminal segment. Segment of fifth leg, as in other pedigerous segments, with dorsal epimeralike lateral expansions. Urosome comprising .45 of total body length. Genital segment expanded laterally, dorsally with dis-

FIGS. 27–39: *Anthessius lighti*, new species. The scales accompanying certain figures represent 0.1 mm. Female: 27, habit, dorsal; 28, habit, lateral; 29, egg sack; 30, lateral part of segment of fourth leg and adjoining structures, dorsal view; 31, antennule; 32, antenna; 33, oral area; 34, mandible; 35, maxillule; 36, maxilla; 37, maxilliped; 38, fifth leg and lateral portion of genital segment; 39, caudal ramus. Legend: *B*. base of fourth leg; *E*. epimeron of segment of fourth leg; *L*. labrum; *M*. mandible; *P*. maxilliped; *R*. protuberance of unknown significance at base of fourth leg; *U*. maxillule; *V*, segment of fifth leg; *X*. maxilla.

tinctive structures marking apertures of oviducts and sites of attachment of egg sacks (Fig. 38). Egg sack (Fig. 29) about .35 of total body length, containing several hundred small eggs.

Antennule (Fig. 31) essentially 7-segmented, but with complicated articulation and integumental modification between second and third segments, so as to suggest either coalescence or incipient separation of an additional minute segment. Approximate proportional lengths of segments, basal to distal: Segment I, 3; II, 7; III, 1.5; IV, 5; V, 3.5; VI, 1; VII, 1. Setae, varying in length and count per segment: Segment I, 4 setae; II, 7 setae near base of segment, 8 around distal end; III, 5 setae, 1 belonging to section suggesting a free segment; IV, 3 setae; V, 4 setae, 1 aesthete; VI, 2 setae, 1 aesthete; VII, about 5 setae, 3 on basal prominence of segment, apparently 2 setae and 1 aesthete apical.

Antenna (Fig. 32) with segmental composition obscured by flexures, involving integumental folds, and torsions, probably 3-segmented. Basal segment with partial distal articulation, 1 short external seta apically. Second segment with very complicated distal articulation, 1 short seta distally and externally inserted. Terminal segment short, with cuticularized ridges and folds and with very broad distal margin furnishing insertion for 4 elaborately articulated clawlike elements and 2 large setae. Another larger seta inserted midway between group of claws and apical setae. Small seta at external distal corner. A subapical group of 4 small setae of diverse lengths. Total elements: 4 claws, 8 setae.

Mouthparts compactly and intricately arranged in oral area (Fig. 33). Labrum of 2 conspicuous lobes, overlying entirely blades of mandibles, and much of distal parts of maxillae.

Mandible (Fig. 34) a flat, unsegmented plate, with cuticularized anterior and posterior margins. Appendage terminating in long lashlike blade with complicated marginal ornamentation. Two most basal elements of ornamentation flat platelike structures, compound apically and articulating with margin of appendage. Remainder of ornamentation a long row of graduated denticles, about 15 of them of conspicuous size. On anterior margin articulated a long lashlike auxiliary seta with conspicuous marginal ornamentation. All of outer margin bearing graduated row of spinules, distal two-thirds of inner margin with short spinules. Between apical lash and auxiliary seta a small articulated cuticular piece, subtriangular in outline.

Maxillule (Fig. 35) of characteristic type for the genus, an elongate lobe with flaring apex. On apex a spine and far laterally a seta. A medial apical indentation setting off a blunt median subapical lobe. Margins of appendage much sclerotized. Apical spine subtended by cuticular spinous processes and spinules.

Maxilla (Fig. 36) with very long diagonal articulation with body surface, resulting in characteristic basal segment, on which articulates flattened apical segment, with heavily cuticularized margins. Apex produced in sharp angle anteriorly with toothlike expansions of cuticle forming a medial saw-edge. Four large teeth formed by flangelike protrusions of cuticle. Apex produced as very small spinelike processes, 1 on each side of most distal tooth. Inserted at base of angle of curvature of this segment and lying on surface, an articulated, short, stout spine.

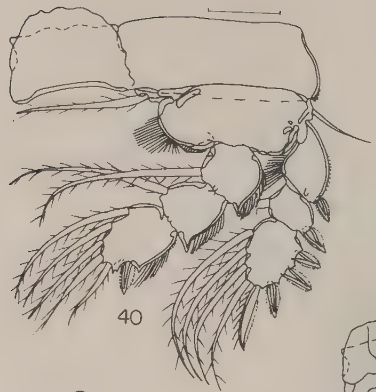
Maxilliped (Fig. 37) fairly long, a prominent mouthpart, as seen in general habitus of mouth area (Fig. 33), but with little development of segmentation or ornamentation. Three segments suggested by folds and flexures of integument. Basal 2 segments not ornamented. Terminal segment with 2 apical setules.

First legs (Fig. 40) with well-developed bimerous protopodites, yoked by substantial intercoxal plate. Basal width of basipodite less than width of distal margin of coxopodite, so medial seta of coxopodite inserted on free portion of margin. Small spinules forming ornament on lateral distal corner of coxopodite. Coxopodite seta relatively long, extending medially, and with its length equal to width of intercoxal plate. Basipodite with lateral seta proximal to insertion of exopodite and with dense row of cilia on curving medial margin. Exopodite, extending directly, without notable flexure, trimerous. Armature: first segment, 1 lateral spine; second segment, 1 lateral spine, 1 medial seta; third segment, 3 lateral spines, 1 terminal spine, 1 terminal seta, 3 medial setae. First segment with fine spinules on lateral margin, dense row of cilia on medial margin. Proximal 5 spines of ramus each outlined with serrate hyaline flange. Apical spine with external hyaline flange and internal row of cilia. Endopodite flexed medially and proximally. Armature: first segment, 1 medial seta; second segment, 1 medial seta; third segment, 1 lateral spine, set in distinct emargination, 2 apical setae, 3 medial setae. Each segment with row of cilia on lateral margin. Each of 2 basal segments produced at distal lateral corner as spinous cuticular process. Spine of terminal segment subtended by such process, and with outlining hyaline flange. All setae of leg with plumose ciliation.

Second legs (Fig. 41) with well-developed bimerous protopodites yoked by substantial intercoxal plate. Medial seta of coxopodite on medial free portion of border of segment. Seta about as long as width of intercoxal plate. A few spinules at lateral distal corner of coxopodite. Basipodite with lateral seta, medial margin with dense row of cilia. Exopodite, extended directly, without notable flexure, trimerous. Armature: first segment, 1 lateral spine; second segment, 1 lateral spine, 1 medial seta; third segment, 3 lateral spines, 1 terminal spine, 1 terminal seta, 4 medial setae. First segment with row of fine spinules on lateral margin, a few cilia on medial margin. Proximal 5 spines of ramus each outlined with serrate, hyaline flange. Apical spine with external hyaline flange and internal row of cilia. Endopodite flexed medially and proximally. Armature: first segment, 1 medial seta; second segment, 2 medial setae; third segment, 2 lateral spines, set in steplike emarginations, 1 terminal spine, 3 medial setae. Each of 2 basal segments produced at distal lateral corner as spinous cuticular process. Spines of terminal segment subtended by such processes, but these less developed than those of basal segments. Each segment with dense row of cilia on lateral margin. Spines of terminal segment with hyaline flanges. All setae of leg with plumose ciliation.

Third legs (Fig. 42) with well-developed bimerous protopodites yoked by substantial intercoxal plate. Medial seta of coxopodite, about as long as width of plate, inserted on medial free portion of distal border of segment. A few spinules at distal lateral corner of coxopodite. Basipodite with small lateral seta; medial margin with dense row of cilia. Exopodite, extended directly, without notable flexure, trimerous. Armature: first segment, 1 lateral spine; second segment, 1 lateral spine, 1 medial seta; third segment, 3 lateral spines, 1 terminal spine, 1 terminal seta, 4 medial setae. First segment with row of fine spinules on lateral margin, dense row of cilia on medial margin. Second segment with a few cilia on proximal part of medial margin. Proximal 5 spines of ramus each outlined with serrate, hyaline flange. Apical spine with external hyaline flange and internal row of cilia. Trimerous endopodite slightly flexed medially and proximally. Armature: first segment, 1 medial seta; second segment, 2 medial setae; third segment, 3 lateral spines, set in steplike emarginations, 1 terminal spine, 2 medial setae. Each of 2 basal segments produced at distal lateral corners as moderately spinous cuticular process. Spines of terminal segment subtended by such processes, but these less developed than those of basal segments. Each segment with dense row of cilia on lateral margin. Spines of terminal segment with hyaline flanges. All setae of leg with plumose ciliation.

Fourth legs (Fig. 43) with well-developed bimerous protopodites yoked by substantial intercoxal plate. Medial seta of coxopodite small, inserted on somewhat diagonally directed medial free portion of distal border of segment. A few spinules at distal lateral corner of coxopodite. Basipodite with small lateral seta; medial margin with short, dense row of cilia. Exopodite, extended directly, without notable flexure, trimerous. Armature: first segment, 1 lateral spine; second segment, 1 lateral spine, 1 medial seta; third segment, 3 lateral spines, 1 terminal spine, 1 terminal seta, 4 medial setae. First segment with row of fine spinules on lateral margin, cilia on medial margin. Proximal 5 spines of ramus each outlined with serrate, hyaline flange. Apical spine with external hyaline flange and internal row of cilia. Trimerous endopodite with very slight medial flexure. Armature: first segment, 1 medial seta; second segment, 2 medial setae; third segment, 3 lateral spines set in steplike emarginations, 1 terminal spine, 1 medial seta. Medial setae of all segments reduced, that of distal segment very short. Each of basal 2 segments produced moderately at distal lateral corner as small spinous cuticular process. Spines of terminal segment subtended by such proc-



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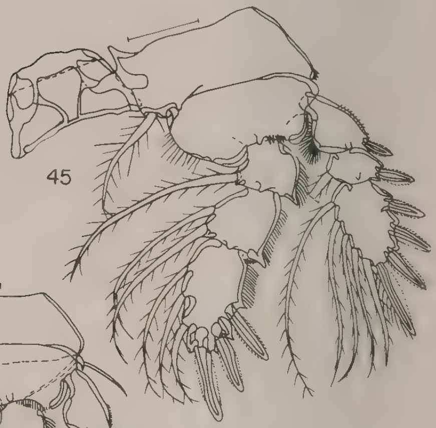

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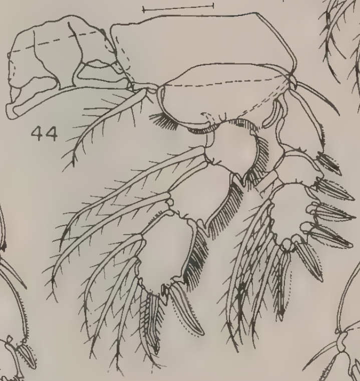

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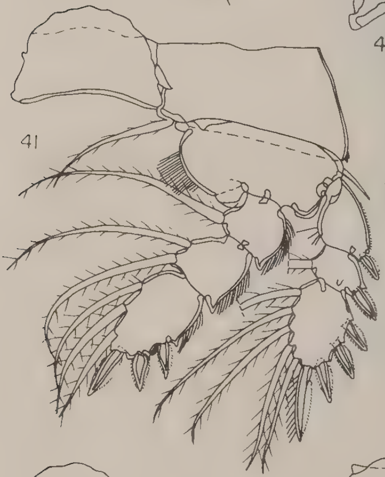

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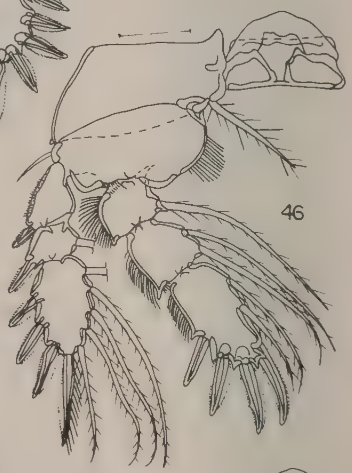

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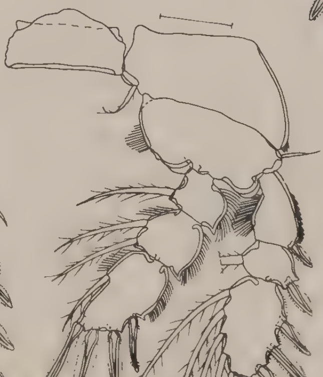

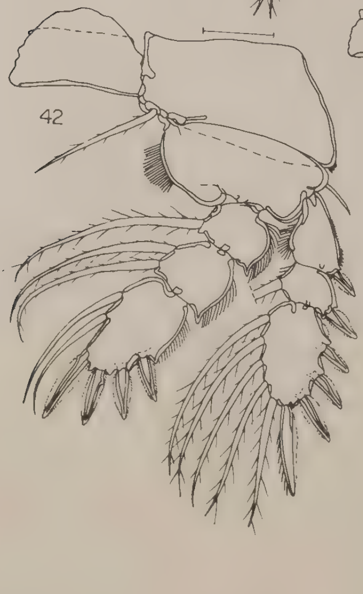

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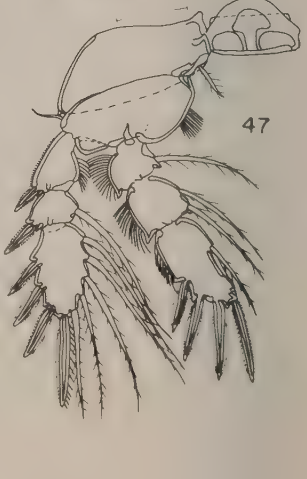

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esses, these less well developed than those of basal segments. Each segment with dense row of cilia on lateral margin, distal 2 segments with medial cilia. Spines of terminal segment with hyaline flanges. All setae of leg with plumose ciliation.

Fifth legs (Fig. 38) with probably 2 segments represented, basal consisting only of expansion on body segment posteriorly and laterally to furnish articulation of distal segment, but with 1 small seta representing armature. Second segment elongate, flat, with cuticularized medial and lateral margins. Length about 4 times greatest width. Armature 3 spines and 1 seta, spines about equally spaced on lateral and terminal margins: 1 lateral spine at about distal three-fourths of lateral margin, 1 lateral spine at about distal .9 of margin; 1 seta inserted close to lateral distal spine; 1 apical spine at medial distal corner. Spines subtended by small groups of spinules and cuticular spinous processes. Spinules of apical spine extending briefly on medial margin to form short row.

Sixth legs probably represented by small setiferous knob (Fig. 38) in depression at aperture of oviduct, located dorsally on lateral expansion of genital segment. Two subequal setules forming armature.

Caudal ramus (Fig. 39) about 2.6 times as long as greatest width and nearly as long as anal segment. Margins with conspicuous cuticular development and some surface ornamentation. Armature consisting of 6 setae. Of apical quartet of setae, medial of central 2 longest, about 3.5 times as long as ramus, adjacent seta 2.2 times length of ramus. Medial apical seta about .73 times as long as ramus; lateral apical seta about .55 times as long as ramus. Lateral marginal seta about .5 as long as ramus, inserted on lateral margin at about distal .6. Dorsal seta short, not quite as long as width of ramus, inserted medially just subapically.

MALE (Figs. 44–58): Body length 2.53 mm., greatest width 0.94 mm., based on 6 specimens. Body (Figs. 48, 49) very generalized cyclopoid in type. Cephalosome bearing first legs, segment of these appendages strongly indicated by indentations. Metasome of free segments of legs 2 to 4. Segment of leg 4 lacking auxiliary lobe-like elements seen in female. Urosome of segments of legs 5, 6, and 4 abdominal segments. Segments of legs 5 and 6 much coalesced in a genital complex containing elongate spermatophores. Segment of leg 5 without epimera.

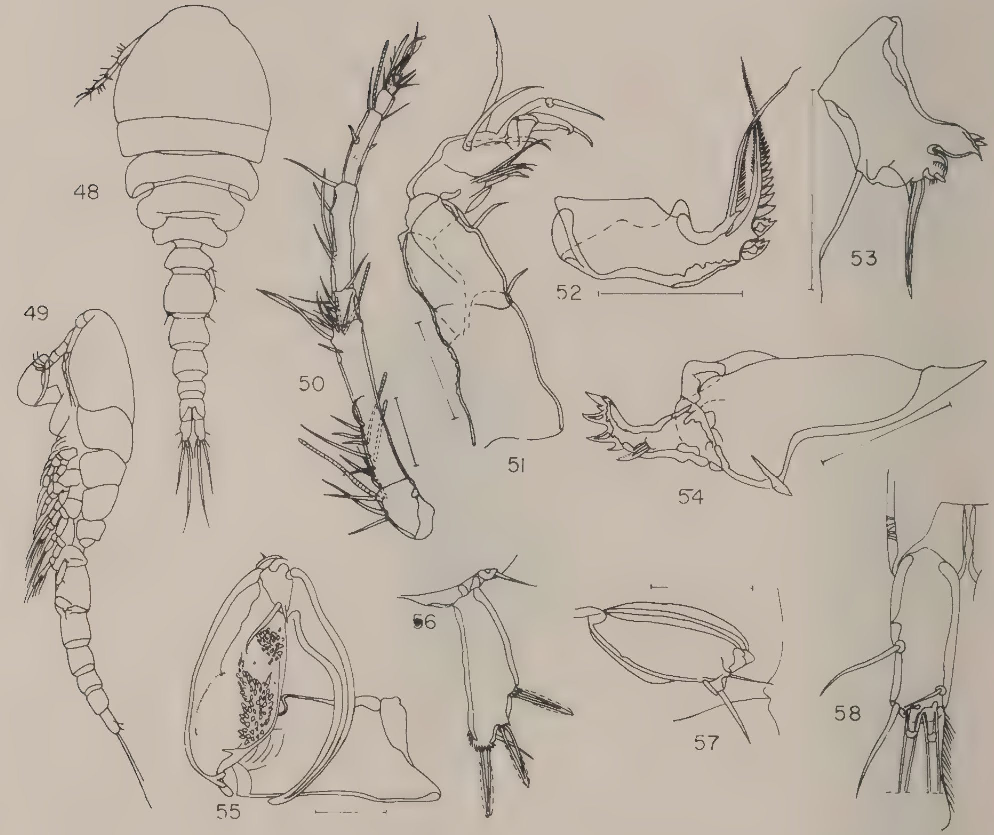
Antennule (Fig. 50) similar in proportions, segmentation and armature to that of female, but with dimorphism expressed in more highly developed aesthetes and greater number of aesthetes. Segment 2 has 2 conspicuous aesthetes accompanying basal group of 7 setae and 1 aesthete accompanying terminal group of 8 setae. Segment 4 has conspicuous aesthete accompanying 3 setae. In segments 5, 6, 7, aesthetes, corresponding to those of the female are present, but tending to be longer.

Antennae and mouthparts, except maxilliped, much as in female. Antenna (Fig. 51); mandible (Fig. 52); maxillule (Fig. 53); maxilla (Fig. 54).

Maxilliped (Fig. 55) highly dimorphic, developed as massive, complicated appendage, possibly trimerous. In mouth area, maxilliped held in characteristic posture. First segment not as long as second, unornamented. Second segment somewhat tapered apically, margin medial in position in normal posture bearing ornamentation serving to act in conjunction with claw-like terminal segment in prehensile function. Medial ornamentation consisting of patches of denticles. In addition, near midpoint of medial margin a short, stout spine. Terminal segment forming very complicated region of articulation on apex of second segment, prolonged as curving claw, longer than second segment. One seta, accompanied by 1 setule, inserted on expanded region of articulation.

Dimorphism also expressed particularly in first legs, remaining swimming legs very similar to those of female. Protopodites and exopodites of first legs (Fig. 44) essentially as in female. Basal segments of endopodites as in female, terminal segment of each with 1 lateral

FIGS. 40–47: *Anthessius lighti*, new species. The scales accompanying certain figures represent 0.1 mm. Female: 40, first leg. 41, second leg; 42, third leg, 43, fourth leg. Male: 44, first leg; 45, second leg; 46, third leg; 47, fourth leg.



FIGS. 48–58: *Anthessius lighti,* new species. The scales accompanying certain figures represent 0.1 mm. Male: 48, habit, dorsal; 49, habit, lateral; 50, antennule; 51, antenna; 52, mandible; 53, maxillule; 54, maxilla; 55, maxilliped; 56, fifth leg; 57, sixth leg; 58, caudal ramus.

spine, 1 apical spine, 1 apical seta, 3 medial setae, apical spine representing a seta of the female appendage. Leg 2 (Fig. 45), leg 3 (Fig. 46), leg 4 (Fig. 47) in general aspect and ornamentation essentially similar to female.

Fifth leg (Fig. 56) very similar to that of female in general structure and ornamentation. Shorter in proportion to width, length equalling about 3 times greatest width.

Sixth legs (Fig. 57) ventrolateral on genital segment, involved in very complicated manner with structure of reproductive opening. Most obviously representative of appendage a small prominence bearing 2 setae, the more medial with an articulating base.

Caudal rami (Fig. 58) with no striking differences from those of female.

REMARKS: This species is named for S. F. Light. The species is distinguished from others of the genus in the key above. Some of its distinctive features may turn out to occur in other species when more anatomical details are known in the genus. The complement of aesthetes on the antennule of the male does not occur in *A. nortoni* and *A. fitchi,* also West Coast forms, but is found in *A. arenicolus* and *A. teissieri* of Europe. The accessory protuberances of the fourth pedigerous segment have not so far been reported from any other species.

Anthessius nortoni, new species
Figs. 59–91

TYPES: Holotypic female, USNM 103304, allotypic male, USNM 103305, paratypes, USNM 103306; paratypes in author's collection. Type locality, San Juan Island, Washington, from *Diadora aspera* (Eschscholtz).

SPECIMENS EXAMINED: From *D. aspera:* Culver's Point, San Juan Island, Washington, intertidal, July 5, 1952, many specimens, females, males, developmental stages, including holotype, allotype. Off Reed Rock, San Juan Channel, Washington, dredged, 92 m., July 2, 1953, many specimens, females, males, developmental stages. Salmon Beach, Tacoma Narrows, Washington, intertidal, May 14, 1953, many specimens, females, males.

The description below and the illustrations are based on a number of specimens, some unmounted, some whole mounts, some temporarily mounted dissections, some permanently mounted dissections. Holotype and allotype are permanently mounted dissections.

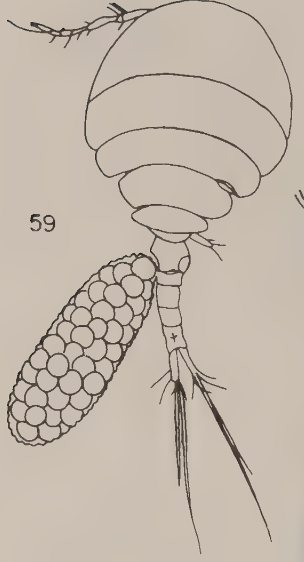
DESCRIPTION: Female (Figs. 59–75): Body length 1.28 mm., greatest width .63 mm., averages from 10 specimens. Body (Fig. 59) broad, of rather generalized cyclopoid contours, with thoracic and abdominal regionalization fairly emphatic. Cephalosome a complex bearing appendages through first swimming legs and comprising .34 of total body length, measured from apex of cephalosome to end of a caudal ramus. Segment of first legs strongly indicated by indentations and grooves, but mass of segment firmly coalesced with more anterior mass of body. Cephalosome and metasome together comprising a forebody of almost circular outline. On anterior margin, apex of head protruded as slight bulge between bases of widely separated antennules (Fig. 60). No rostrum, apical ventral region of head a wide flattened expanse between bases of antennules and antennae. Metasome including pedigerous segments of second through fourth legs, with general body articulation between segments of legs 4 and 5. Urosome a complex including segment of legs 5, genital segment and 3 additional abdominal segments, considering element of anal opening and supporting caudal rami as terminal segment. Urosome comprising .4 of total body length. Genital segment expanded laterally, dorsally with distinctive structures marking apertures of oviducts and sites of attachment of egg sacks (Fig. 61). Last abdominal segment with double row of spinules at midline on anterior ventral surface and with spinule rows on margins subtending each caudal ramus (Fig. 62). Egg sack about .6 as long as body, much exceeding tip of caudal ramus. Many small eggs in each egg sack.

Antennule (Fig. 71) essentially 7-segmented, but with a complicated articulation and integumental modification between second and third segments, so as to suggest either coalescence or incipient separation of an additional minute segment. Proportional lengths of segments, basal to distal: Segment I, 1.5; II, 3; III, 1; IV, 3; V, 2; VI, 1; VII, 1. Setae varying in length; count per segment: Segment I, 4 setae; II, 7 setae near base of segment, 8 around distal end; III, 5 setae, 1 belonging to section suggesting a free segment; IV, 3 setae; V, 4 setae, 1 aesthete; VI, 2 setae, 1 aesthete; VII, 7 setae and 1 aesthete, 4 setae on basal prominence of segment, 3 setae and aesthete apical.

Antenna (Fig. 63) short and stout, with segmental composition much obscured by flexures involving integumental folds and torsions of one region of appendage on adjoining regions, probably essentially 3-segmented. Basal segment fairly clear-cut, apical articulation diagonal, 1 short external seta apically. Second segment with very complicated distal articulation, this proceeding diagonally across appendage; 1 short seta externally inserted. Terminal segment with cuticularized ridges and folds and with very broad distal margin furnishing insertion for 4 elaborately articulated clawlike elements, varying much in size, and 2 setae. Another seta near distal margin. A subapical group of 4 setae of diverse lengths. Total elements: 4 claws, 7 setae.

Mouthparts compactly and intricately arranged in oral area (Fig. 64). Labrum of 2 conspicuous lobes, overlying entirely blades of mandibles, and much of distal parts of maxillae.

Mandible (Fig. 65) a flat plate, with very cuticularized anterior and posterior margins. Appendage terminating in long lashlike blade with complicated marginal ornamentation: Two



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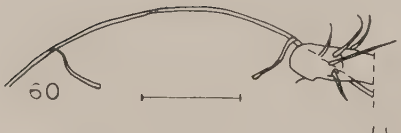

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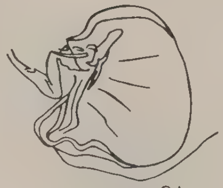

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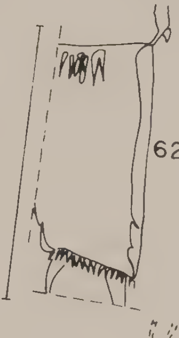

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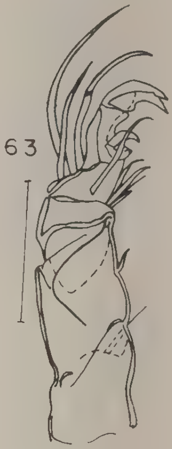

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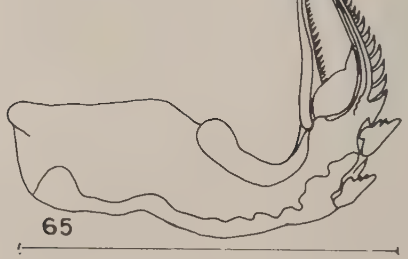

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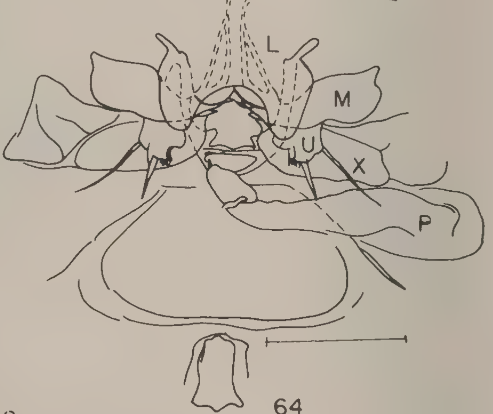

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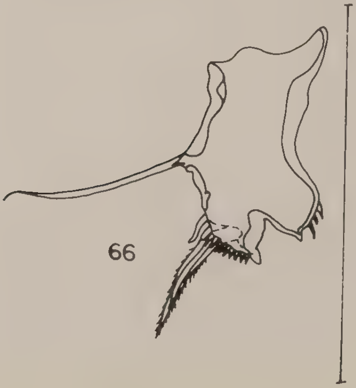

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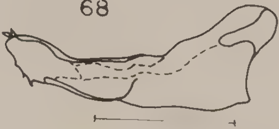

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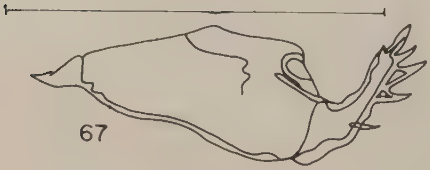

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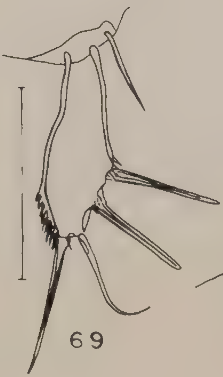

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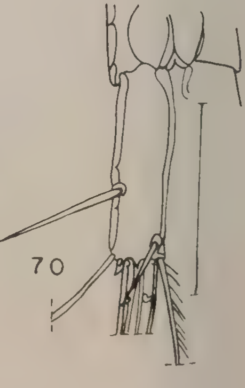

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most basal elements of ornamentation flat toothlike structures, compound apically and articulating with margin of appendage; remainder of ornamentation a long row of graduated denticles, about 15 of them of conspicuous size. On anterior margin articulated a long lashlike auxiliary seta with outer margin bearing graduated row of spinules on proximal third; inner margin without spinules. Between apical lash and auxiliary seta a subtriangular cuticular piece, flat and platelike.

Maxillule (Fig. 66) of characteristic type of the genus, an elongate plate with lobed apex. On apex a spine; at midpoint of lateral margin a seta. An apical indentation setting off a blunt median subapical lobe. Margins of appendage much sclerotized. A few spinules on median lobe and row of graduated spinules subtending apical spine.

Maxilla (Fig. 67) with very long articulation with body, resulting in characteristic basal segment, on which articulates flattened apical segment, with heavily cuticularized margins. Apex produced in sharp angle anteriorly with toothlike expansions of cuticle forming a medial sawedge. Four large teeth formed by flangelike protrusions of cuticle. Inserted at base of angle of curvature of this segment and lying on surface, a small, articulated spine.

Maxilliped (Fig. 68) fairly long, a prominent mouthpart, as seen in general habitus of mouth area, but with little development of segmentation or ornamentation. Three segments suggested by folds and flexures of integument. Terminal segment with 2 apical setules. Margins cuticularized and produced into 2 spinulelike protrusions.

First legs (Fig. 72) with well-developed bimerous protopodites, yoked by substantial intercoxal plate. Basal width of basipodite less than width of distal margin of coxopodite, so medial seta of coxopodite inserted on free portion of margin. Small spinules forming ornamentation on lateral corner of coxopodite. Coxopodite seta very long, extending rather medially and distally, and with its length more than width of intercoxal plate. Basipodite with long lateral seta proximal to insertion of exopodite and with row of cilia on distal margin. Exopodite with slight medial flexure, trimerous. Armature: first segment, 1 lateral spine; second segment, 1 lateral spine, 1 medial seta; third segment, 3 lateral spines, 1 terminal spine, 1 terminal seta, 3 medial setae. First segment with large spinules on lateral margin, row of cilia on medial margin. Proximal 5 spines of ramus each outlined with serrate hyaline flange. Apical spine with external hyaline flange and internal row of cilia. Endopodite flexed medially and proximally. Armature: first segment, 1 medial seta; second segment, 1 medial seta; third segment, 1 lateral spine, set in distinct emargination, 1 lateral seta, 1 apical seta, 3 medial setae. Each of 2 basal segments produced at distal lateral corner as spinous cuticular process. Spine of terminal segment subtended by such process, and with outlining hyaline flange. Each segment with row of cilia on lateral margin. All setae of leg with plumose ciliation.

Second legs (Fig. 73) with well-developed bimerous protopodites yoked by substantial intercoxal plate. Medial seta of coxopodite on medial free portion of border of segment. Seta about as long as width of intercoxal plate. A row of spinules at distal lateral corner of coxopodite. Basipodite with short lateral seta; terminal margin with rows of cilia. Exopodite trimerous. Armature: first segment, 1 lateral spine; second segment, 1 lateral spine, 1 medial seta; third segment, 3 lateral spines, 1 terminal spine, 1 terminal seta, 4 medial setae. First segment with row of stout spinules on lateral margin, cilia on medial margin. Proximal 5 spines of ramus each outlined with serrate, hyaline flange. Apical spine with external hyaline flange and internal row of cilia. Endopodite flexed medially and proximally. Armature: first segment, 1 medial seta; second segment, 2 medial setae; third segment, 2 lateral spines, set in steplike emarginations, 1 terminal spine, 3 medial

FIGS. 59–70: *Anthessius nortoni*, new species. The scales accompanying certain figures represent 0.1 mm. Female: 59, habit, dorsal; 60, ventral apical region of cephalosome; 61, structures at genital aperture; 62, one side of anal segment showing ornamenting spinules; 63, antenna; 64, oral area; 65, mandible; 66, maxillule, 67, maxilla; 68, maxilliped; 69, fifth leg; 70, part of anal segment and caudal ramus. Legend: *L*, labrum; *M*, mandible; *P*, maxilliped; *U*, maxillule; *X*, maxilla.

setae. Each of 2 basal segments produced at distal lateral corner as spinous cuticular process. Spines of terminal segment subtended by such processes, but these much less developed than those of basal segments. Each segment with dense row of cilia on lateral margin. Spines of terminal segment with hyaline flanges. All setae of leg with plumose ciliation.

Third legs (Fig. 74) with well-developed bimerous protopodites yoked by substantial intercoxal plate. Medial seta of coxopodite, slightly longer than width of plate, inserted on medial free portion of distal border of segment. A few spinules at distal lateral corner of coxopodite. Basipodite with lateral seta; terminal margin with rows of cilia. Exopodite, extended directly, without notable flexure, trimerous. Armature: first segment, 1 lateral spine; second segment, 1 lateral spine, 1 medial seta; third segment, 3 lateral spines, 1 terminal spine, 1 terminal seta, 4 medial setae. First segment with row of spinules on lateral margin, cilia on medial margin. Proximal 5 spines of ramus each outlined with serrate, hyaline flange. Apical spine with external hyaline flange and internal row of cilia. Trimerous endopodite flexed medially and proximally. Armature: first segment, 1 medial seta; second segment, 2 medial setae; third segment, 3 lateral spines, set in steplike emarginations, 1 terminal spine, 2 medial setae. Each of 2 basal segments produced at distal lateral corner as moderately small, spinous cuticular process. Spines of terminal segment subtended by such processes, but these less developed than those of basal segments. Each segment with dense row of cilia on lateral margin. Spines of terminal segment with hyaline flanges. All setae of leg with plumose ciliation.

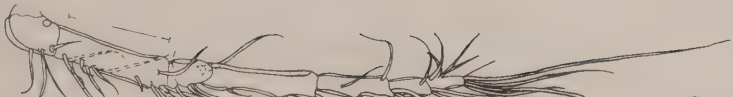
Fourth legs (Fig. 75) with well-developed bimerous protopodites yoked by substantial intercoxal plate. Medial seta of coxopodite very small, inserted on somewhat diagonally directed medial free portion of distal border of segment. A few spinules at distal lateral corner of coxopodite. Basipodite with small lateral seta, medial margin with row of cilia. Exopodite, extended directly, without notable flexure, trimerous. Armature: first segment, 1 lateral spine; second segment, 1 lateral spine, 1 medial seta; third segment, 2 lateral spines, 1 terminal spine, 1 terminal seta, 4 medial setae. First segment with row of spinules on lateral margin, cilia on medial margin. Proximal 4 spines of ramus each outlined with serrate, hyaline flange. Apical spine with external hyaline flange and internal row of cilia. Trimerous endopodite with very slight flexure. Armature: first segment, 1 medial seta; second segment, 2 medial setae; third segment, 3 lateral spines set in steplike emarginations, 1 terminal spine, 1 medial seta. Each of basal 2 segments produced moderately at distal lateral corner as small spinous cuticular process. Each spine of terminal segment subtended by such process, these less well developed than those of basal segments. All segments with dense rows of cilia on lateral margins. Spines of terminal segment with hyaline flanges. All setae of leg with plumose ciliation.

Fifth legs (Fig. 69) with probably 2 segments represented, basal consisting only of expansion on body posteriorly and laterally on segment of legs to furnish articulation of distal segment, but with 1 small seta representing armature. Second segment elongate, flattened, with cuticularized medial and lateral margins. Shape highly distinctive, basal fourth much constricted, with abrupt flare to level of first spine. Length about 3.2 times greatest width. Armature 3 spines and 1 seta, about equally spaced on lateral and terminal margins: 1 lateral spine at about distal .7 of lateral margin, 1 lateral spine at about distal .8 of margin; 1 seta at lateral distal corner; apical spine at medial distal corner. Spines subtended by small groups of spinules. Short row of spinules on distal fourth of medial margin.

Sixth legs probably represented by small setiferous knob (Fig. 61) in depression at aperture of oviduct, located dorsally on lateral expansion of genital segment. One small setule forming armature.

Caudal ramus (Fig. 70) about 3 times as long

FIGS. 71–79: *Anthessius nortoni,* new species. The scales accompanying certain figures represent 0.1 mm. Female: 71, antennule; 72, first leg; 73, second leg; 74, third leg; 75, fourth leg. Male: 76, first leg; 77, second leg; 78, third leg; 79, fourth leg.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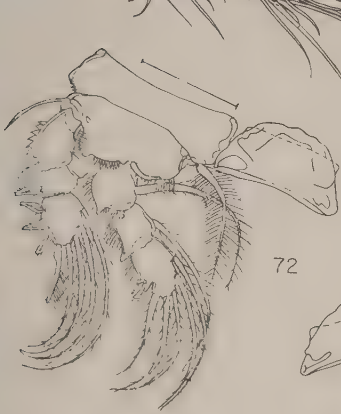
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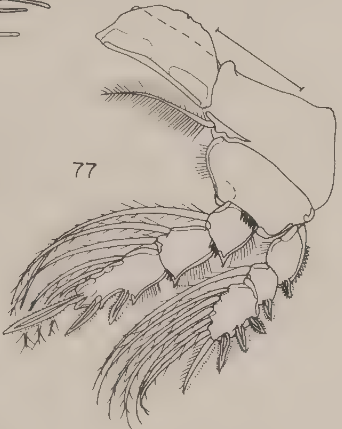
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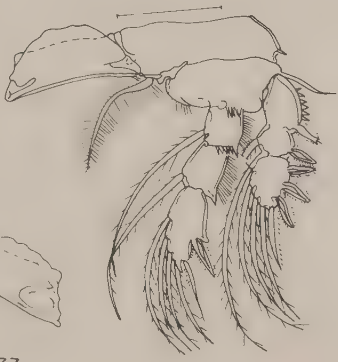
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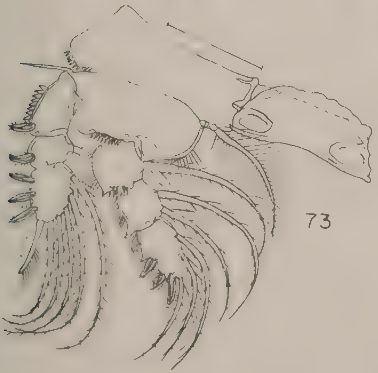
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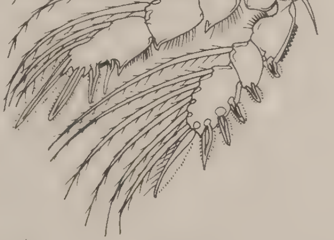
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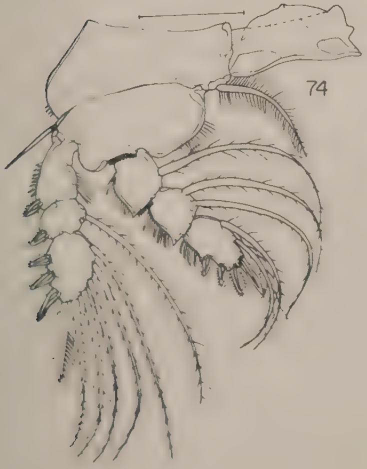
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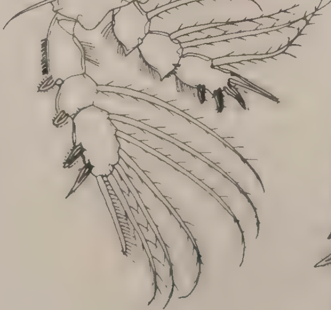
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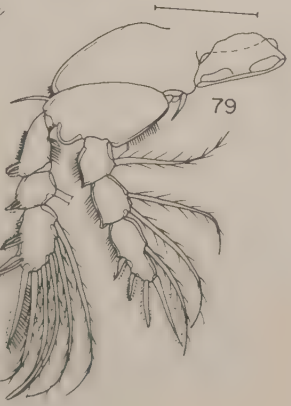
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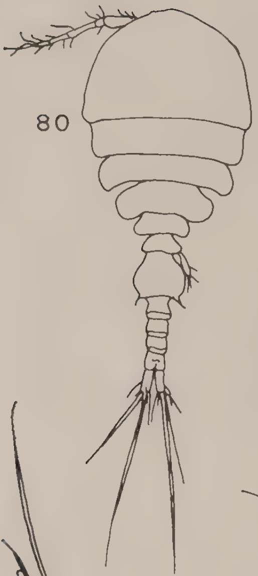
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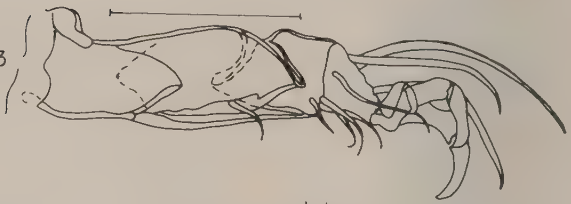
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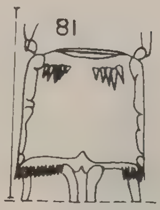
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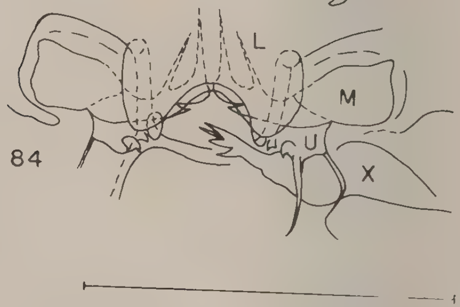
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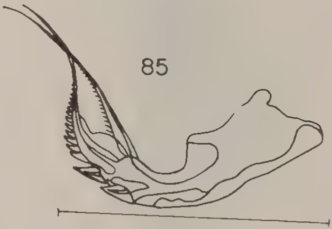
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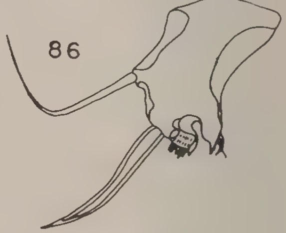
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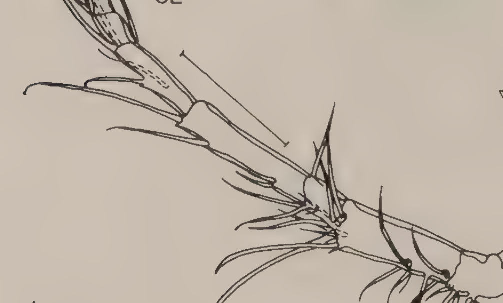
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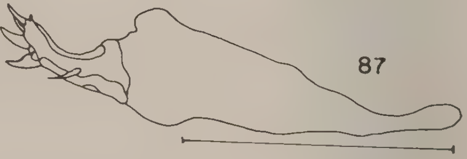
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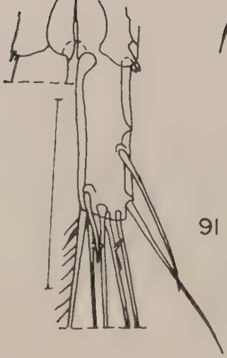
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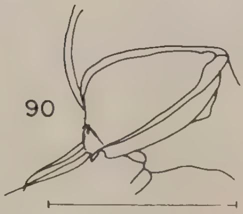
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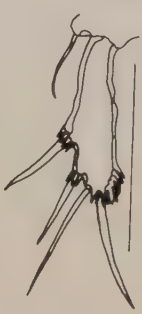
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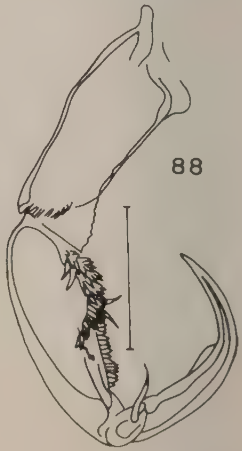
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as greatest width and 1.2 times as long as anal segment. Margins with conspicuous cuticular development. Armature 6 setae. Of apical quartet of setae, medial of central 2 longest, about 6.3 times as long as ramus, adjacent seta 3.5 times length of ramus. Medial apical seta about 1.6 times as long as ramus; lateral apical seta about .8 times as long as ramus. Lateral marginal seta short, about .7 times as long as ramus, inserted on lateral margin about at distal .6. Dorsal medial seta short, about as long as width of ramus, inserted just subapically.

MALE (Figs. 76–91): Body length 1.25 mm., greatest width .56 mm., averages from 10 specimens. Body (Fig. 80) very similar to that of female in size and aspect, but approaching a little more closely to generalized cyclopoid type. Cephalosome bearing first legs, segment of these indicated by very slight marginal indentations. Metasome of free segments of legs 2 to 4. Urosome of segments of legs 5, 6, and 4 abdominal segments, including element bearing anus and caudal rami. Segments of legs 5 and 6 much coalesced to form a genital complex, through which extend elongate spermatophores. Ornamentation of anal segment (Fig. 81) much as in female.

Antennule (Fig. 82) similar in proportions, segmentation and armature to that of female, no particular dimorphism expressed.

Antennae and mouthparts, except maxilliped as in female. Antenna (Fig. 83); oral area (Fig. 84); mandible (Fig. 85); maxillule (Fig. 86); maxilla (Fig. 87).

Maxilliped (Fig. 88) highly dimorphic, developed as massive, complicated appendage, probably trimerous. First segment about as long as second, with row of fine spinules on distal margin. Second segment somewhat tapered apically, margin medial in position of normal posture of appendage bearing characteristic ornamentation serving to act in conjunction with clawlike terminal segment in prehensile function, this consisting of patches of long denticles. In addition, near midpoint of medial margin 2 short, stout spines. Terminal segment forming very complicated region of articulation on apex of second segment, prolonged as curving claw, longer than second segment. One seta inserted on expanded region of articulation with segment 2.

Dimorphism also expressed particularly in first and third legs, remaining swimming legs very similar to those of female. Protopodites and exopodites of first legs essentially as in female. Basal segments of endopodites as in female, terminal segment of each with lateral spine, 1 apical spine, 1 apical seta, 3 medial setae, very long apical spine representing a seta of female appendage (Fig. 76). Leg 2 (Fig. 77) in general aspect and ornamentation essentially similar to that of female. Leg 3 (Fig. 78) showing slight dimorphism in that most proximal lateral spine of terminal segment of endopodite has characteristic shape, a basal knob, angled posture, and lacks outlining hyaline flange of other spines of rami. Leg 4 (Fig. 78) as in female.

Fifth leg (Fig. 89) very similar to that of female in general structure. Length about 3 times greatest width. Accessory ornamentation of spinules more highly developed than in female.

Sixth legs (Fig. 90) ventrolateral on genital segment, involved in very complicated manner with structure of reproductive opening. Most obviously representative of appendage a small prominence bearing 2 unequal setae, the more medial with a well-developed articulating base.

Caudal rami (Fig. 91) very similar to those of female.

REMARKS: This form is named for John R. Norton. The species occurs very commonly in association with its typical host in Washington Sound, Puget Sound, and also on the outer rocky ocean coast of Washington, in the Cape Flattery Region. The usual infestation consists of fair numbers of the copepod, ranging to several dozen. They wander freely in the rather capacious respiratory cavity of the host, sometimes emerging from the dorsal aperture or moving over the foot and other fleshy parts. They are

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FIGS. 80–91: *Anthessius nortoni*, new species. The scales accompanying certain figures represent 0.1 mm. Male: 80, habit, dorsal; 81, anal segment, 82, antennule; 83, antenna; 84, oral area; 85, mandible; 86, maxillule; 87, maxilla; 88, maxilliped; 89, fifth leg; 90, sixth leg; 91, part of anal segment and caudal ramus. Legend: *L*, labrum; *M*, mandible; *U*, maxillule; *X*, maxilla.

usually readily detected if the host is held in sea water for observation. There has been no interaction so far detected between the copepod and the other extremely commonly occurring associate of *D. aspera,* the polynoid worm *Arctonoë vittata* (Grube). The large limpets of the genus *Acmaea,* living in the same environment as the host, sometimes will be found to have a specimen of *A. nortoni* in the respiratory cavity, but I feel that present evidence does not justify considering this as a regularly occurring association. The typical host should be further explored for this associate over its considerable range; I suspect the copepod will be found to have a wide distribution. This is one of the very small species of *Anthessius,* and in many regards it shows resemblance to the common European *A. arenicolus* and *A. teissieri.* However, it is distinctive anatomically, as expressed in part in the key to species above. It is the first member of the genus so far reported in association with an aspidobranch gastropod.

Anthessius fitchi, new species
Figs. 92–125

TYPES: Holotypic female, USNM 103301, allotypic male, USNM 103302, paratypes, USNM 103303; paratypes in author's collection. Type locality, Carpinteria, California, from *Chaceia ovoidea* (Gould).

SPECIMENS EXAMINED: From *C. ovoidea:* Carpinteria, California, November 11, 1954, J. E. Fitch, many specimens, females, males, including holotype and allotype.

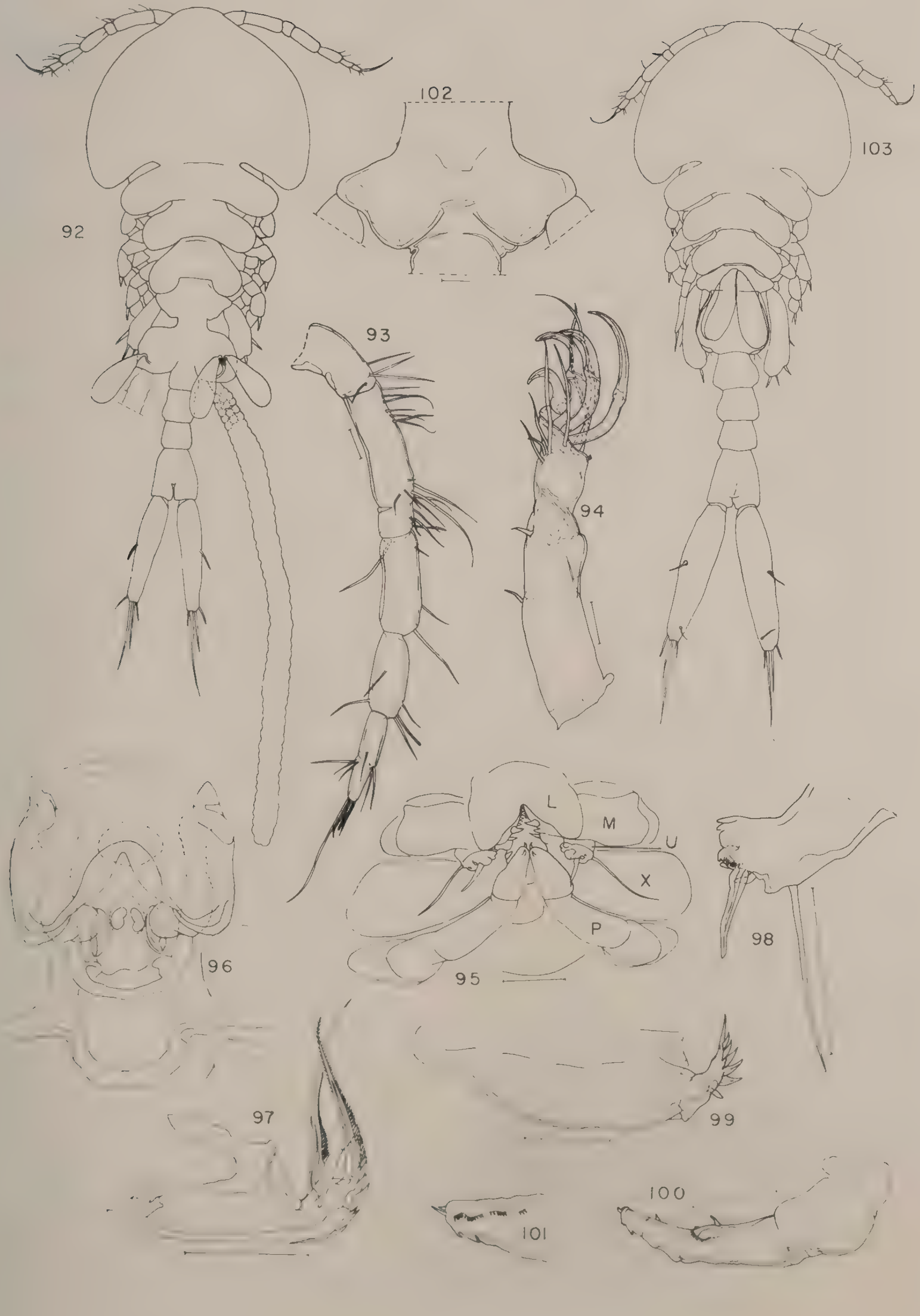
Carpinteria, California, January 1, 1956, J. E. Fitch, 50 + specimens.

From *Zirfaea pilsbryi* Lowe: Fossil Point, Coos Bay, Oregon, July 23, 1959, 1 ♀.

The description below and the illustrations are based on a number of specimens, some unmounted, some whole mounts, some temporarily mounted dissections, some permanently mounted dissections. Holotype and allotype are permanently mounted dissections.

DESCRIPTION: Female (Figs. 92–102, 104–110): Body length 5.8 mm. (5.6–6.1), greatest width 2.1 mm. (2.0–2.3), based on 10 specimens. Body (Fig. 92) of this gigantic species of most distinctive habitus, retaining only general overall cyclopoid contours. Salient characteristics of habitus consist in much expanded outline of cephalosome, elongate antennules, much expanded lateral winglike epimera of thoracic segments, lateral expansions of genital segment, elongate and distally widened anal segment, and elongate, flattened and widened caudal rami. Not continuously present on adults, but of such distinctive nature as to contribute to definite aspect of characteristic habitus, elongate stringlike egg sacks and persistently attached stalked spermatophores. Cephalosome a fused complex bearing appendages through first swimming legs without any demarcation of segment of these latter. Cephalosome comprising .25 of total body length. Apically a slight protrusion between bases of antennules. Ventrally, area between antennular bases somewhat bulged and outlined by cuticular thickenings, but not developed as a proper rostrum (see Fig. 117 for this feature in male). Metasome of 3 pedigerous segments, each with widely flaring lateral winglike epimera, those of first metasomal segment much the widest, those of next 2 segments successively diminishing. Urosome a complex including segment of legs 5, genital segment and 3 additional abdominal segments, considering element bearing anal opening and caudal rami as terminal segment. Urosome comprising .55 of total body length. Segment of fifth legs (Fig. 102) lacking epimera, but with lateral expansions of entire mass of segment. Anterior and posterior margins of segment of about same width, greatest lateral extent about 2.33 times width of anterior margin. Each lateral protrusion also somewhat inflated, with resultant structures extending almost to center of segment. Fifth legs inserted apically on each expansion. Genital segment also of very distinctive outline, with two widely extending lateral ex-

FIGS. 92–103: *Anthessius fitchi,* new species. The scales accompanying certain figures represent 0.1 mm. Female: 92, habit, dorsal; 93, antennule; 94, antenna; 95, oral area; 96, labrum and supporting structure of oral area with appendages removed; 97, mandible; 98, maxillule; 99, maxilla; 100, maxilliped; 101, apex of maxilliped; 102, segment of fifth legs, dorsal. Male: 103, habit, dorsal. Legend: *L.* labrum; *M.* mandible; *P,* maxilliped; *U,* maxillule; *X,* maxilla.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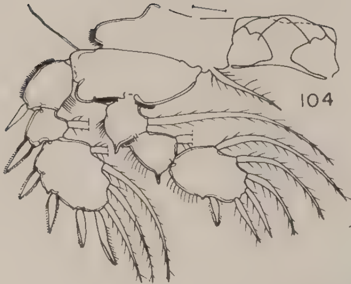
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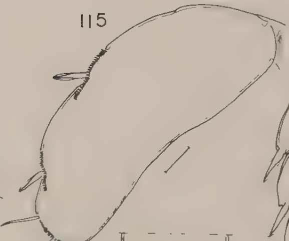
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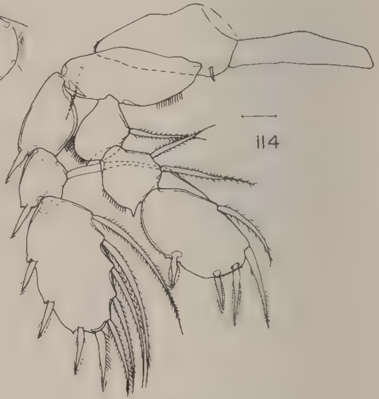
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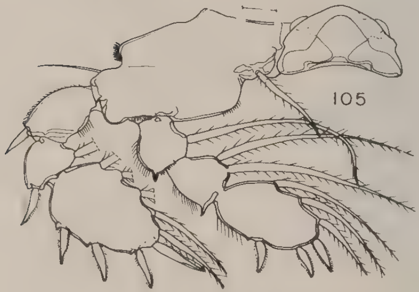
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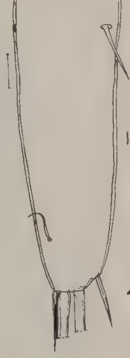
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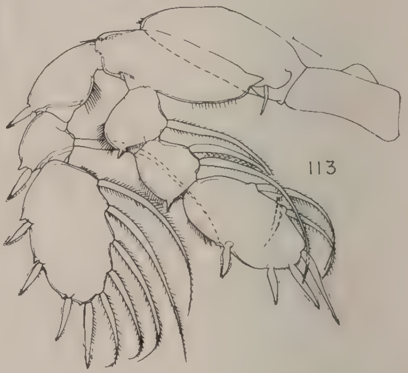
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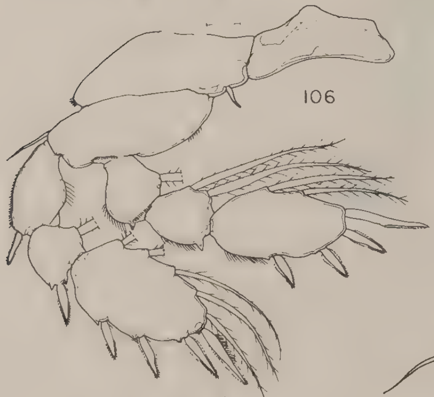
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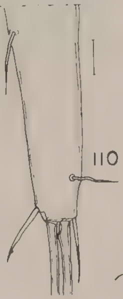
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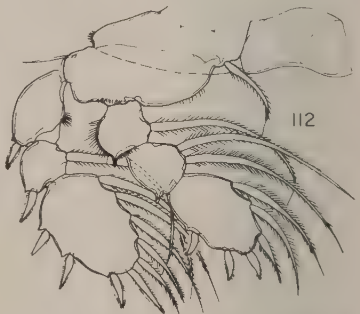
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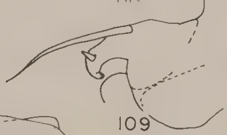
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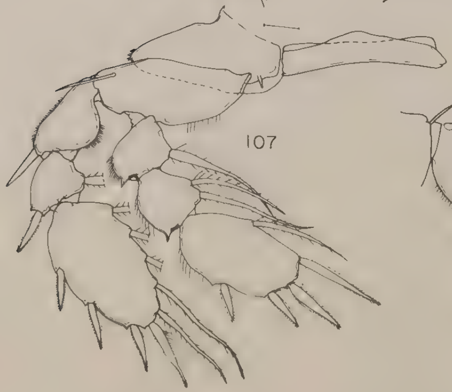
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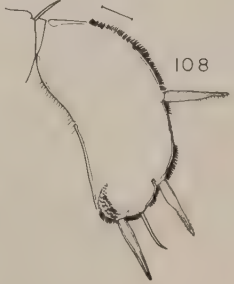
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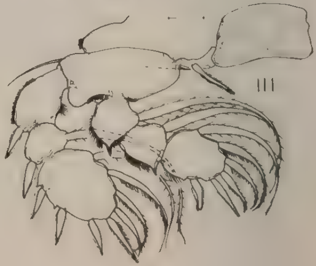
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pansions. Anterior and posterior margins of segment about equal width, greatest lateral extent over 3 times width of anterior margin. Median mass of segment not notably intruded on by reproductive structures, these occupying most of each strong lateral protrusion. Dorsally on each lateral process 1 or 2 spermatophores usually seen in persistent attachment Each spermatophore elongate, ovoid, length about 3 times greatest width, with gradual taper to apical filiform attachment stalk, about .3 times as long as spermatophore proper.

Elongate egg sacks, about .75 as long as the body and with width only .05 length, hence of pronounced filiform aspect, attaching near posterior margin of each process of genital segment.

In remainder of urosome anterior 2 of 3 abdominal segments subequal, much smaller than anal segment. Latter almost 2 times as long as next anterior and with distinctive flaring outline, greatest width, just subterminal, 1.5 times width of anterior margin of segment.

Antennule (Fig. 93) long, somewhat flattened, 7-segmented, fifth segment with notable expansion of outline. Approximate proportional lengths of segments, basal to distal: Segment I, 2.5; II, 4; III, 1; IV, 3.3; V, 2.7; VI, 1.7; VII, 1.4. Setae varying in length. Count of setae, per segment: Segment I, 4 setae; II, 7 setae near base of segment, 8 around distal end; III, 5 setae; IV, 3 setae; V, 4 setae, 1 aesthete; VI, 2 setae, 1 aesthete; VII, 6 setae, 3 on basal prominence of segment, 3 setae and 1 aesthete apical.

Antenna (Fig. 94) with segmental composition much obscured by flexures, involving integumental folds, and torsions of regions of appendage, probably essentially 3 segments. Basal segment not clearly defined, apical articulation incomplete, 1 short external seta apically. Second segment with very complicated distal articulation, this proceeding diagonally across appendage; 1 short seta on external margin. Terminal segment with cuticularized ridges and folds and with very broad distal margin furnishing insertion for 4 elaborately articulated clawlike elements and 2 setae. Another seta near distal margin. A subapical group of 4 setae of diverse lengths. Total elements: 4 claws, 7 setae.

Mouthparts compactly and intricately arranged in oral area (Fig. 95). Labrum with 2 lobes, overlying blades of mandibles. Basal structures of labrum complex, associated with other sclerotized pieces located postorally, to form an intricate mouth apparatus (Fig. 96).

Mandible (Fig. 97) a flat plate, with very cuticularized anterior and posterior margins. Appendage terminating in long lashlike blade with complicated marginal ornamentation. Most basal elements of ornamentation flat platelike structures articulating with margin of appendage. Remainder of ornamentation a long graduated row of denticles. On anterior margin of mandible articulated a long lashlike auxiliary seta with conspicuous marginal cuticularization. Basal two-thirds of outer margin bearing graduated row of spinules. Between apical lash and auxiliary seta a flat cuticular piece with indented distal margin, forming an outer lobe with acuminate apex and an inner lobe with rounded terminal outline.

Maxillule (Fig. 98) of characteristic type for genus, an elongate lobe with flaring apex. On apex a more medial spine and very long lateral seta. A medial apical indentation setting off a blunt medial subapical lobe. Margins of appendage much sclerotized, produced into spinelike cuticular processes apically and on medial lobe.

Maxilla (Fig. 99) with very long articulation with body, resulting in characteristic basal segment, on which articulates flattened apical segment, with heavily cuticularized margins. Apex produced in sharp angle anteriorly with toothlike expansions of marginal cuticle forming a medial saw-edge. Five to 7 large teeth formed by flangelike protrusions of cuticle. Apex produced as more elongate spinelike process. Inserted at base of angle of curvature of this segment and lying on surface, a stout, short articulated spine.

FIGS. 104–116. *Anthessius fitchi*, new species. The scales accompanying certain figures represent 0.1 mm. Female. 104, first leg; 105, second leg; 106, third leg; 107, fourth leg; 108, fifth leg; 109, sixth leg; 110, caudal ramus. Male: 111, first leg; 112, second leg; 113, third leg; 114, fourth leg; 115, fifth leg; 116, caudal ramus.

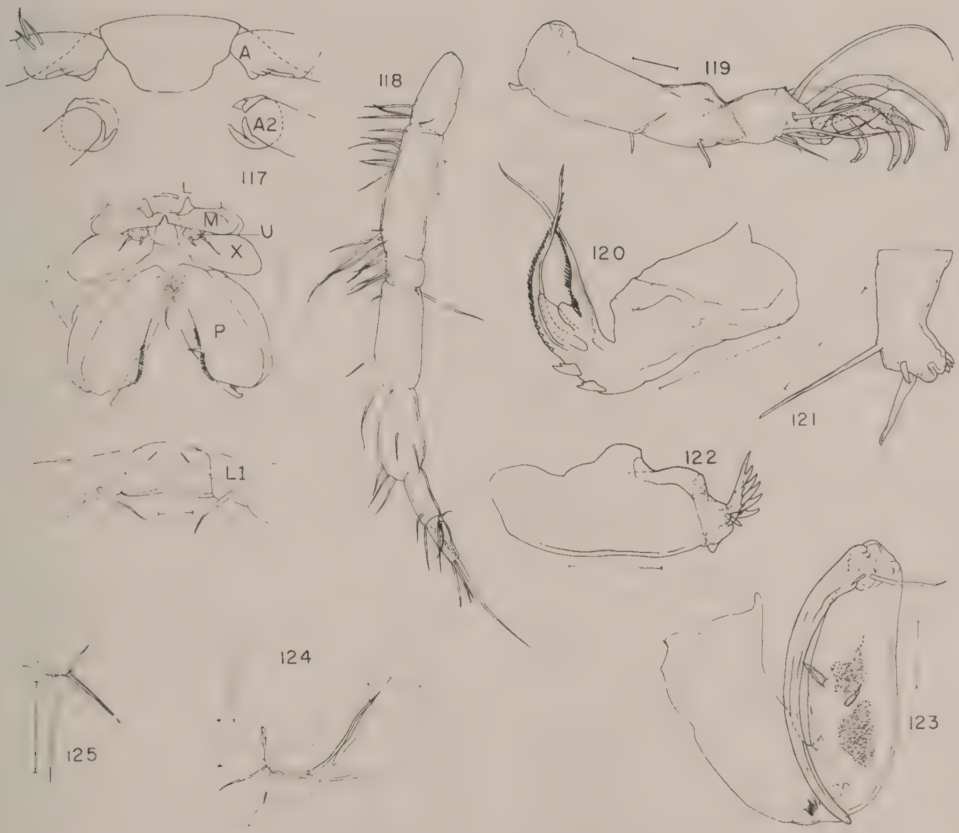
Maxilliped (Fig. 100) fairly long, a prominent mouthpart, as seen in general habitus of mouth area, but with little development of segmentation or ornamentation. Three segments suggested by folds and flexures of integument. Basal segment fairly well defined, unornamented. Second segment ornamented with 1 marginal setule and an arching row of spinules. Terminal segment with 2 apical setules and an interrupted row of spinules on the surface (Fig. 101). Margin cuticularized and produced into 2 or more spinulelike protrusions.

Legs 1 to 4 very characteristic for the species and unlike those of any other form so far described in the genus in marked flattening and exaggerated development of terminal segments of rami as broad laminae. Armature and ornamentation essentially identical with that of other species. A peculiar type of cuticular ornament distributed over various body elements, seemingly highly distinctive for the species. Each element of this ornamentation apparently a small cylinder with flat end, the whole of fairly soft consistency and protruding like a tube from surface of body. A large number of these over ventral surfaces of wide epimeral expansions of cephalosome, a few on each epimeron of metasomal segments, a few on each basipodite, some on terminal segment of each ramus of each leg, some on fifth leg, fairly large numbers forming rows down middle of surface of each caudal ramus.

First legs (Fig. 104) with well-developed bimerous protopodites, yoked by substantial intercoxal plate. Basipodite laterally offset on coxopodite, so medial seta of coxopodite inserted on free portion of terminal margin. Coxopodite seta extending rather more medially than distally, and with its length slightly less than width of intercoxal plate. Distal lateral corner of coxopodite with row of spinules. Basipodite with small lateral seta proximal to insertion of exopodite and with short rows of cilia on distal margin. Exopodite trimerous; armature: first segment, 1 lateral spine; second segment, 1 lateral spine, 1 medial seta; third segment, 3 lateral spines, 1 terminal spine, 1 terminal seta, 3 medial setae. First segment with fine spinules on lateral margin and row of cilia on medial margin. Proximal 5 spines of ramus each outlined with serrate hyaline flange. Apical spine with external entire hyaline flange and internal row of cilia. Endopodite flexed medially and proximally, trimerous. Armature: first segment, 1 medial seta; second segment, 1 medial seta; third segment, 1 lateral spine, set in slight emargination, 2 apical setae, 3 medial setae. Three most distal setae reduced in length. Each of basal 2 segments of ramus produced at distal lateral corner as spinous cuticular process. Spine of terminal segment subtended by minute spinous process, and with outlining hyaline flange. Each segment with row of cilia on lateral margin. All setae of leg with plumose ciliation.

Second legs (Fig. 105) with well-developed bimerous protopodites yoked by substantial intercoxal plate. A row of spinules at distal lateral corner of coxopodite. Medial seta of coxopodite on medial free portion of border of segment. Seta about as long as width of intercoxal plate. Basipodite with long lateral seta; terminal margin with rows of cilia. Exopodite, flexed and at angle to protopodite, trimerous. Armature: first segment, 1 lateral spine; second segment, 1 lateral spine, 1 medial seta; third segment, 3 lateral spines, 1 terminal spine, 1 terminal seta, 4 medial setae. First segment with row of fine spinules on lateral margin, cilia on medial margin. Proximal 5 spines of ramus each outlined with serrate, hyaline flange. Apical spine with apical hyaline flange and internal row of cilia. Endopodite flexed medially and proximally, trimerous. Armature: first segment, 1 medial seta; second segment, 2 medial setae; third segment, 2 lateral spines, set in slight emarginations, 1 terminal spine, 3 medial setae. Setae of terminal segment progressively reduced. Each of 2 basal segments produced at distal lateral corner as spinous cuticular process. Basal spine of terminal segment subtended by such process, but this much less developed than those of basal segments. Each segment with row of cilia on lateral margin. Spines of terminal segment with hyaline flanges. All setae of leg with plumose ciliation.

Third legs (Fig. 106) with well-developed bimerous protopodites yoked by substantial intercoxal plate. Small medial seta of coxopodite inserted on medial free portion of distal border of segment. A few spinules at distal lateral corner of coxopodite. Basipodite with lateral seta;



Figs. 117–125: *Anthessius fitchi,* new species. The scales accompanying certain figures represent 0.1 mm. Male: 117, ventral view of mid-region of cephalosome; 118, antennule; 119, antenna; 120, mandible; 121, maxillule; 122, maxilla; 123, maxilliped; 124, sixth leg and reproductive aperture; 125, setae of sixth leg. Legend: *A,* antennule; *A2,* antenna; *L,* labrum; *L1,* base of first leg; *M,* mandible; *P,* maxilliped; *X,* maxilla.

terminal and medial margins with rows of cilia. Exopodite, with medially curving flexure, trimerous. Armature: first segment, 1 lateral spine; second segment, 1 lateral spine, 1 medial seta; third segment, 3 lateral spines, 1 terminal spine, 1 terminal seta, 4 medial setae. First segment with row of fine spinules on lateral margin, cilia on medial margin. Proximal 5 spines of ramus each outlined with serrate, hyaline flange. Apical spine with apical hyaline flange and internal row of cilia. Trimerous endopodite slightly flexed medially and proximally. Armature: first segment, 1 medial seta; second segment, 2 medial setae; third segment, 3 lateral spines, set in slight emarginations, 1 terminal spine, 2 medial setae. Setae of terminal segment reduced. Each of 2 basal segments produced at distal lateral corner as moderately small spinous cuticular process. Basal spine of terminal segment subtended by such process, but less developed than those of basal segments. Each segment with row of cilia on lateral margin. Spines of terminal segment with hyaline flanges, apical spine with flange only on distal lateral margin. All setae of leg with plumose ciliation.

Fourth legs (Fig. 107) with well-developed bimerous protopodites yoked by widely extending, short proximal to distal, intercoxal plate. Medial seta of coxopodite very small, inserted on medial free portion of distal border of segment. A few spinules at distal lateral corner of coxopodite. Basipodite with lateral seta. Exopodite with slight flexure, trimerous. Armature: first segment, 1 lateral spine; second segment, 1 lateral spine, 1 medial seta; third segment, 3 lateral spines, 1 terminal spine, 1 terminal seta, 4 medial setae. First segment with row of fine spinules on lateral margin, cilia on medial margin. Proximal 5 spines of ramus each outlined with serrate, hyaline flange. Apical spine with apical flange and internal row of cilia. Trimerous endopodite with medial flexure. Armature: first segment, 1 medial seta; second segment, 2 medial setae; third segment, 3 lateral spines set in emarginations, 1 terminal spine, 1 medial seta. Medial setae of all segments reduced, that of distal segment very short. Each of basal 2 segments produced moderately at distal lateral corner as small spinous cuticular process. Each spine of terminal segment subtended by such process, these less well-developed than those of basal segment. Each segment with row of cilia on lateral margin. Spines of terminal segment with hyaline flanges. All setae of leg with plumose ciliation.

Fifth legs (Fig. 108) with probably 2 segments represented, basal involved in expansion on segment of body posteriorly and laterally to furnish articulation for distal segment, with 1 small seta representing armature. Second segment elongate, very wide, flattened, with cuticularized medial and lateral margins. Length about 2 times greatest width. Armature 3 spines and 1 seta, spines about equally spaced on lateral and terminal margins: 1 lateral spine at about distal half of lateral margin, 1 lateral spine at about distal .9 of margin; apical spine at medial distal corner. Short, slender seta between terminal 2 spines, somewhat closer to apical spine. Spines subtended by small groups of spinules. A row of spinules on proximal third of medial margin and a row on most of lateral margin. Several short rows of spinules forming dense patch at apical medial corner.

Sixth legs probably represented by setiferous curving process (Fig. 109) at aperture of oviduct, located dorsally on lateral expansion of genital segment. Armature 1 relatively well-developed seta and 1 short, tapered, stout spinule.

Caudal ramus about 4.5 times as long as greatest width and about 2 times as long as anal segment. Shape most characteristic, a flat lamina expanding to greatest width at about proximal third, gradually tapering to apex, which is half as wide as greatest width. Margins with conspicuous cuticular development. Armature 6 setae (Fig. 110). Of apical quartet of setae, medial of central 2 longest, about .8 times as long as ramus, adjacent seta about .4 times length of ramus. Medial apical seta about .16 times as long as ramus; lateral apical seta about .16 times as long as ramus. Lateral marginal seta short, about .7 times as long as ramus, inserted slightly proximal to midpoint of lateral margin. Dorsal medial seta short, slender, about .1 times length of ramus, inserted subapically, at about distal .9 of ramus. Length of caudal ramus 1.1 mm. (1.0–1.1) and greatest width .23 mm. (.20–.25), averages for 10 specimens.

MALE (Figs. 103, 111–125): Body length 6.0 mm. (5.6–6.2), greatest width 2.1 mm. (1.9–2.3), averages from 10 specimens. Body shape (Fig. 103) of same distinctive form as that of female, slightly larger overall, with larger fifth legs and larger caudal rami. Cephalosome equivalently expanded in outline, without superficial indication of included segment of first legs. Antennules elongated and flattened. Cephalosome much the widest body region. Ventrally at apex a bulgelike protrusion (Fig. 117), not an actual rostrum. Three segments of metasome each with distinctive expanded lateral epimera, as in female. Urosome 6-segmented, very characteristic in structure, by enormous size of fifth legs, uniquely developed anal segment and caudal rami. Segments of legs 5 and 6 much coalesced in a genital complex containing elongate paired spermatophores. Segment of leg 5 widest segment of urosome, fifth legs borne far laterally and each lying along and parallel with margin of next posterior segments. Fifth leg reaching to middle of third urosomal segment. Segment of leg 6 longest segment of urosome, with some lateral expansion, this involving only very gradual taper from anterior margin of segment. Anal segment, as in female, with flaring outline, and supporting enormous, elongate, flattened caudal rami.

Antennule (Fig. 118) markedly similar in proportions, segmentation and armature to that of female, all elements seeming to correspond in the two sexes. Antennae (Fig. 119) also like those of female.

Oral area (Fig. 117) with characteristic aspect, only differing from that of female because of great development of dimorphic maxillipeds, these appearing as most conspicuous element in complex of mouthparts.

Mandible (Fig. 120) essentially as in female, some minute differences in details of ornament, possibly as much expression of individual difference as of dimorphism. Maxillule (Fig. 121) almost exactly as in female. Maxilla (Fig. 122) as in female.

Maxilliped (Fig. 123) highly dimorphic, developed as massive, complicated appendage, apparently 3-segmented. First segment not as long as second, about .75 as long, unornamented, except for distal lateral clump of spinules. Second segment somewhat tapered apically, margin medial in position in normal posture of appendage bearing characteristic ornamentation serving to act in conjunction with clawlike terminal segment in prehensile function. Medial ornamentation consisting of dense patches of denticles. In addition, near midpoint of medial margin a short, stout spine and another spine at same level on inner surface of segment. Terminal segment forming very complicated region of articulation on apex of second segment, prolonged as curving claw, slightly longer than second segment. One long seta, accompanied by 1 setule, inserted on expanded region of articulation with segment 2.

Dimorphism expressed also in first legs, remaining swimming legs very similar to those of female. Protopodites and exopodites of first legs (Fig. 111) essentially as in female. Basal segments of endopodites as in female, terminal segment of each with lateral spine, 1 apical spine, 1 apical seta, 3 medial setae, the apical spine representing a seta of female appendage. Leg 2 (Fig. 112), leg 3 (Fig. 113), leg 4 (Fig. 114) in general aspect and ornamentation essentially similar to those of female.

Fifth legs (Fig. 115) only resembling those of female in general structure and ornamentation, but of different outline and proportionately much longer. Length equaling about 3 times greatest width. Distal spines and seta much more widely spaced than in female. Marginal ornamentation of spinules less developed than in female.

Sixth legs (Fig. 124) ventrolateral on genital segment, involved in very complicated manner with structure of reproductive opening. Most obviously representative of appendage a small prominence bearing 2 setae (Fig. 125), the more medial with well-developed articulating base.

Caudal rami similar in outline and general features to those of female, armature (Fig. 116) also corresponding, but rami of greater overall size and proportionately slightly wider in male. Length 1.3 mm. (1.2–1.4), greatest width .3 mm. (.295–.305), averages from 10 specimens.

REMARKS: The species is named for John E. Fitch. This gigantic copepod is by far the most distinctive form in the genus and stands much separated from all other species by the elaborate development of the body processes and the form of most appendages. Perhaps its unique habitus deserves greater taxonomic emphasis than specific designation, but I cannot see any additional information to be provided by the designation of a monotypic taxon for this form. Except for absolute size, the antennae and mouthparts are very consistent with those of other species. In the other appendages the numerical complement of segments and elements of armature are entirely the same as for other species, but in outlines and dimensions the structure remains unique. The typical host is a giant piddock, boring burrows in substantial rock. The copepods occur over the general body surface of the host and in its burrows, according to the collector. The distribution of this host is apparently a limited one. An indication of broader distribution of the copepod exists in the single specimen, collected in Oregon, 1959, from *Zirfaea,* a large boring mollusk, closely related to *Chaceia.*

SUMMARY: Five species of *Anthessius* are described in detail, two of these, *A. hawaiiensis* (Wilson) and *A. navanacis* (Wilson), being redescribed from type material. These occur in Hawaii and Southern California, respectively. New species described are *A. lighti* and *A. fitchi*

from California and *A. nortoni* from Washington. Hosts for these species are a nudibranch, *Pleurobranchus,* for *A. hawaiiensis,* tectibranchs, *Navanax* and *Aplysia,* for *A. navanacis* and *A. lighti,* a pelecypod, *Chaceia* for *A. fitchi,* and an aspidobranch gastropod *Diadora* for *A. nortoni.* These findings, added to previous records, increase the impression that the genus is composed of species characteristically associated with a variety of molluscan hosts.

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Hawaiian Helminths, Part III
New Opecoelid Trematodes

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Reprinted from PACIFIC SCIENCE
October, 1960

Reprinted from PACIFIC SCIENCE, *vol. XIV, no. 4, October, 1960*

Hawaiian Helminths, Part III
New Opecoelid Trematodes[1]

W. E. MARTIN[2]

THE OPECOELID TREMATODES described in this paper were collected from Hawaiian fishes by the author during a sabbatical leave spent mainly at the Hawaii Marine Laboratory of the University of Hawaii. A recent review of the family Opecoelidae by Skrjabin (1958) includes, among others, keys to the genera *Opecoelus* and *Coitocaecum* which contain four of the five species described in the present paper. The fifth species is assigned to the genus *Pseudopecoeloides.* A sixth species in this family, *Dactylostomum caballeroi,* collected in Hawaii is described elsewhere (Martin, in press).

The specimens described here were fixed in Heidenhains' solution, stained with either Mayer's paracarmine or Celestin Blue B, and mounted in H–S–R mounting medium.

All measurements are expressed in millimeters.

EXPLANATION OF FIGURES

All drawings were made with the aid of a camera lucida. Abbreviations used: *A,* acetabulum; *C,* cecum; *Ci,* cirrus; *CS,* cirrus sac; *E,* excretory vesicle; *G,* genital pore; *M,* metraterm; *O,* ovary; *P,* prostate; *S,* seminal vesicle; *T,* testis; *V,* vitellaria.

Coitocaecum Nicoll, 1915

Coitocaecum banneri n. sp.
Figs. 1, 2

SPECIFIC DIAGNOSIS: Based on seven specimens. Body smooth, oval, length 1.414–1.855, av. 1.683, greatest width 0.399–1.071, av. 0.858; oral sucker subterminal, length 0.21–.256, av. 0.241, width 0.196–.238, av. 0.217; acetabulum, length 0.308–.392, av. 0.348, width 0.252–.357, av. 0.329; prepharynx very short; pharynx oval, muscular, 0.096–.112, av. 0.106 long, and 0.088–.112, av. 0.096 wide; esophagus nearly as long as pharynx, glandular; ceca united near posterior end of body; gonads in posterior third of body, ovary pretesticular, smooth to weakly three-lobed, immediately to right of midventral line, 0.148–.224, av. 0.2 transversely, and 0.084–.126, av. 0.105 anteroposteriorly; seminal receptacle lacking; Laurer's canal present; Mehlis gland diffuse, lightly staining, immediately anterior to ovary; proximal uterine coils contain many sperm, uterine coils mainly intercecal and between ovary and acetabulum; metraterm short; eggs operculate, yellow, 0.048–.058, av. 0.056 long, and 0.027–.032, av. 0.03 wide; vitellaria richly developed, extending from about midesophageal level to posterior end of body, usually separated anteriorly but joining posteriorly, invading intercecal zone; testes postovarian, tandem to oblique, smooth to indented, posterior testis usually larger than anterior, anterior testis 0.231–.504, av. 0.334 long, and 0.108–.252, av. 0.167 wide, posterior testis 0.175–.49, av. 0.335 long, and 0.112–.291, av. 0.216 wide; seminal vesicle saccular, terminating shortly anterior to or slightly overlapping the acetabulum; cirrus sac short, cirrus weakly developed; genital pore ventral, on left side of body at postpharyngeal level; excretory bladder tubular, reaching to ovary, opening at posterior end of body.

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[1] These studies were aided by a contract between the Office of Naval Research, Department of the Navy, and the University of Southern California, NR 165-252.

The opinions or assertions contained herein are the private ones of the author and are not to be construed as official or reflecting the views of the naval service at large.

I wish to thank Drs. A. H. Banner, R. W. Hiatt, and L. D. Tuthill of the Marine Laboratory and the Department of Zoology and Entomology, University of Hawaii, for the use of laboratory space and equipment.

Contribution No. 140, Hawaii Marine Laboratory, University of Hawaii. Manuscript received March 19, 1959.

[2] Biology Department and Allan Hancock Foundation, University of Southern California.

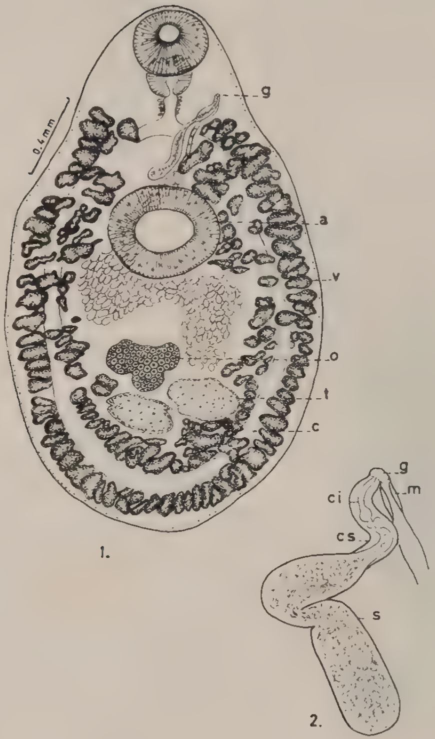


FIG. 1. *Coitocaecum banneri,* ventral view.
FIG. 2. *C. banneri,* terminal genital organs.

HOST: *Thalassoma duperrey* (Quoy and Gaimard), a wrasse. Hawaiian name: hinalea lauwili.

Three of seven fish infected; maximum number of worms, 4.

LOCATION: Gall bladder.

LOCALITY: Kaneohe Bay, Oahu, Hawaii.

TYPE SPECIMEN: *Coitocaecum banneri,* deposited as no. 569, Hancock Parasitology Collection.

Coitocaecum hawaiensis n. sp.
Figs. 3, 4

SPECIFIC DIAGNOSIS: Based on four specimens. Body smooth, spindle-shaped, length 0.801–1.435, av. 1.136, maximum width 0.385–.469, av. 0.418; oral sucker subterminal, 0.107–.13, av. 0.119 long, and 0.096–.12, av. 0.11 wide; acetabulum near mid-body, 0.192–.256, av. 0.223 transversely, and 0.166–.192, av. 0.82 anteroposteriorly; prepharynx short; pharynx oval, muscular, 0.08–.104, av. 0.089 long, and 0.064–.072, av. 0.071 wide; esophagus usually shorter than pharynx; ceca extend laterally and posteriorly to unite a short distance posterior to testes; gonads in posterior third of body, ovary pretesticular, on right side of body, oval to triangular, smooth, 0.084–.088, av. 0.086 long, and 0.056–.08, av. 0.071 wide; Mehlis gland immediately anterior to ovary; Laurer's canal present; seminal receptacle lacking; coils of uterus confined to intercecal area between gonads and acetabulum; metraterm about half the length of the cirrus sac; eggs yellow, operculate 0.048–.051, av. 0.05 long, and 0.024–.027, av. 0.026 wide; vitellaria richly developed, extending from pharynx level to near posterior end of body, invading intercecal zone, uniting anteriorly and posteriorly; testes immediately post-ovarian, tandem, smooth to slightly irregular, anterior testis 0.16 long, and 0.056–.064, av. 0.06 wide; posterior testis 0.128–.137, av. 0.132 long, and 0.08–.112, av. 0.093 wide; seminal vesicle saccular, terminating shortly anterior to or slightly overlapping acetabulum, surrounded by large cells with large nuclei; cirrus sac nearly as long as seminal vesicle and twice as long as metraterm; genital pore ventral, on left side of body at pharyngeal level, excretory bladder tubular, reaching to ovarian level, opening at posterior end of body.

HOST: *Thalassoma duperrey* (Quoy and Gaimard), a wrasse. In one of seven fish.

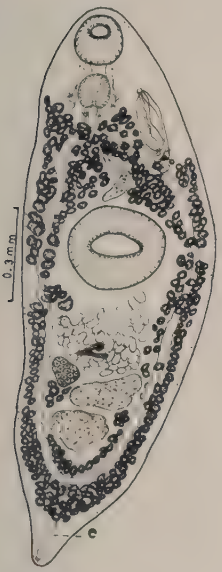
LOCATION: Gall bladder.

LOCALITY: Kaneohe Bay, Oahu, Hawaii.

TYPE SPECIMEN: *Coitocaecum hawaiensis,* deposited as no. 5610, Hancock Parasitology Collection.

Coitocaecum norae n. sp.
Figs. 5, 6

SPECIFIC DIAGNOSIS: Based on one specimen. Body smooth, oval, 1.05 long and 0.476 wide; oral sucker 0.144 by 0.128; acetabulum diameter 0.187; prepharynx short; pharynx oval, 0.048 long and 0.04 wide; esophagus approximately as long as pharynx, glandular, ceca extend lat-



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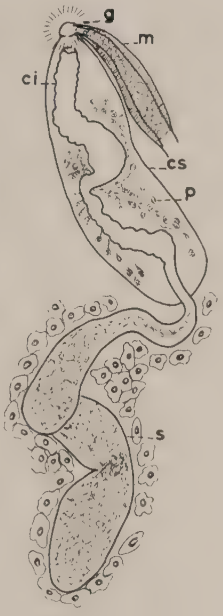

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FIG. 3. *Coitocaecum hawaiensis*, ventral view.
FIG. 4. *C. hawaiensis*, terminal genital organs.

erally and posteriorly to unite near posterior end of body; gonads in posterior half of body, ovary pretesticular, three-lobed; Laurer's canal present; seminal receptacle lacking; Mehlis gland indistinct; uterine coils few, between ovarian and acetabular levels; metraterm short, relatively thick-walled; vitellaria extend from pharyngeal level to near posterior end of body, invading intercecal zone; eggs yellow, operculate, approximately 0.049 long and 0.029 wide; testes tandem, transversely elongate, lobed; seminal vesicle extends posteriorly to anterior margin of acetabulum; cirrus sac about twice as long as metraterm; cirrus weak, about same length as metraterm; common genital pore ventral, on left side of body, at mid-esophageal level; excretory bladder tubular, reaching to ovary, with thicker-walled posterior portion, opening terminally.

HOST: *Ctenochaetus strigosus* (Bennett). One of fourteen fish infected.

LOCATION: Gall bladder.

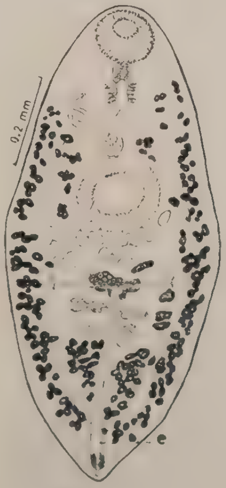
LOCALITY: Kaneohe Bay, Oahu, Hawaii.

TYPE SPECIMEN: *Coitocaecum norae*, deposited as no. 5611, Hancock Parasitology Collection.

The new species of *Coitocaecum* described in this paper are unique in living in the gall bladder, all other species of the genus having been recovered from the digestive tract. *C. banneri* seems to be closest to *C. orthorchis* Ozaki 1929, found in the stomach and intestine of *Tridentiger obscurus* Temminck and Schlegel at Hiroshima, and *Acanthogobius flavimanus* T. and S. from the fish market of Takamatsu City, Japan. Besides the differences of host and location within the host, *C. banneri* has larger suckers, a longer cirrus sac, and smaller eggs than *C. orthorchis*.

Coitocaecum hawaiensis also is close to *C. orthorchis* and *C. banneri*. It differs from both in having a well-developed cirrus sac and cirrus, in having the seminal vesicle surrounded by large cells, and in the union of vitellaria anteriorly.

Coitocaecum norae has lobed, transversely elongate and narrow (anteroposteriorly) testes that distinguish it from all other species of the genus.



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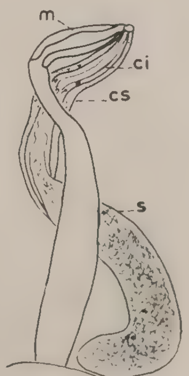

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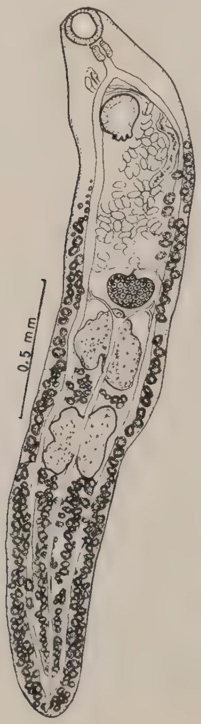
FIG. 5. *Coitocaecum norae*, dorsal view.
FIG. 6. *C. norae*, terminal genital organs.

Opecoelus lanceolatus n. sp.
Figs. 7, 8, 9

SPECIFIC DIAGNOSIS: Based on four specimens. Body elongate, narrow, smooth, 1.86–3.08, av. 2.4 long, and 0.364–.476, av. 0.394 maximum width; oral sucker subterminal 0.096–.112, av. 0.106 long, and 0.096–.112, av. 0.103 wide; acetabulum with five pairs of dactyls or papillae, the three median pairs longer than others, acetabulum 0.16–.172, av. 0.164 long, and 0.16 wide; prepharynx short; pharynx oval, 0.064–.08, av. 0.078 long, and 0.04–.058, av. 0.049 wide; esophagus approximately as long as pharynx; ceca extend laterally and posteriorly to join near the posterior end of body, rectum short, anus ventral, near posterior end of body; gonads in middle third of body, ovary pretesticular, oval to slightly indented; Mehlis gland diffuse, immediately anterior to ovary; Laurer's canal present; seminal receptacle lacking; uterine coils intercecal, mainly between ovary and acetabulum; metraterm short but slightly longer than cirrus sac; vitellaria extend from a short distance posterior to the acetabulum to the posterior end of body where they unite, mainly extracecal but slightly invading intercecal zone anterior to ovary and conspicuously between the testes and posterior to them; eggs yellow, operculate, 0.042–.048, av. 0.047 long, and 0.029–.032, av. 0.031 wide; testes tandem, one or both with indentation in posterior margin, anterior testis 0.179–.288, av. 0.24 long, and 0.09–.238, av. 0.188 wide; posterior testis 0.192–.32, av. 0.232 long, and 0.112–.224, av. 0.184 wide; seminal vesicle elongate, tubular, usually extending posterior to the acetabulum at least the diameter of the latter organ; cirrus sac short, enclosing prostatic cells and a weakly developed cirrus; common genital pore on left side of body, at or near posterior pharyngeal level; excretory vesicle tubular, reaching to or near ovary, opening terminally.



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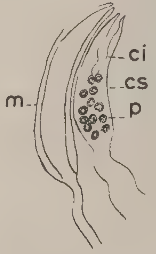

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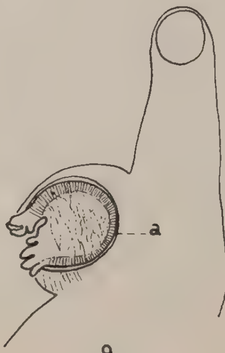


9.

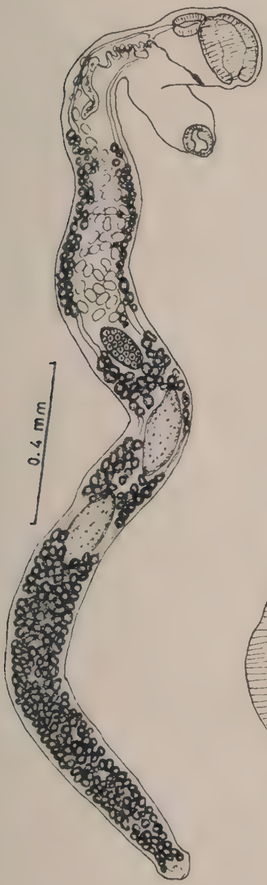
FIG. 7. *Opecoelus lanceolatus,* dorsal view.
FIG. 8. *O. lanceolatus,* terminal genital organs.
FIG. 9. *O. lanceolatus,* side view to show dactyls on acetabulum.

HOST: *Mulloidichthys samoensis* (Gunther), a goatfish. Four of ten fish infected.
LOCATION: Intestine.
LOCALITY: Kaneohe Bay, Oahu, Hawaii.
TYPE SPECIMEN: *Opecoelus lanceolatus,* deposited as no. 5612, Hancock Parasitology Collection.

Opecoelus lanceolatus seems to be closest to *O. xenistii* Manter, 1940, found in the intestine of *Xenistius californiensis* (Steindachner) collected at Tagus Cove, Albemarle Island, Galapagos. It differs from *O. xenistii* in the following ways: the vitellaria do not extend anteriorly as far as the acetabulum, the metraterm is much shorter, and the ovary is not trilobed.

Pseudopecoeloides tenuoides n. sp.
Figs. 10, 11

SPECIFIC DIAGNOSIS: Based on eight specimens. Body elongate, slender, smooth, somewhat constricted at gonad levels, 2.555–5.04, av. 3.47 long, and 0.16–.5, av. 0.3 wide; oral sucker subterminal 0.22–.28, av. 0.243 long, and 0.18–.23, av. 0.193 wide; acetabulum pedunculate



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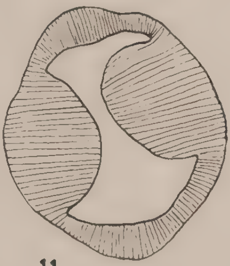

11.

Fig. 10. *Pseudopecoeloides tenuoides.*
Fig. 11. *P. tenuoides,* acetabulum showing pads.

with thick pads, 0.068–.118, av. 0.098 long, and 0.087–.109, av. 0.096 wide; prepharynx short; pharynx 0.087–.124, av. 0.1 long, and 0.65–.081, av. 0.068 wide; esophagus up to two-thirds length of pharynx; ceca proceed laterally and posteriorly to unite with excretory bladder near posterior end of body; gonads in middle third of body; ovary pretesticular, oval to spindle-shaped, smooth, 0.131–.211, av. 0.18 long, and 0.062–.143, av. 0.096 wide; Mehlis gland immediately anterior to ovary; Laurer's canal present; seminal receptacle lacking; uterine coils mainly between ovary and seminal vesicle; metraterm indistinct; eggs oval, operculate, 0.040–.050, av. 0.044 long, and 0.025–.037, av. 0.030 wide; vitellaria well developed beginning a little posterior to the seminal vesicle and extending to near the posterior end of body, interrupted at gonad levels; testes spindle-shaped, smooth, tandem, anterior testis 0.187–.336, av. 0.267 long and 0.093–.146, av. 0.115 wide, posterior testis 0.218–.348, av. 0.292 long, and 0.093–.124, av. 0.111 wide; seminal vesicle tubular with a coiled narrow duct; prostate cells fairly numerous; cirrus rudimentary, a cirrus sac was not observed; genital opening ventral, sinistral, approximately midway between suckers; excretory vesicle tubular extending to or near ovary, opening terminally as a cloaca.

HOST: *Priacanthus cruentatus* (Lacépède). Four of seven fish infected; maximum number of worms, four.

LOCATION: Intestine.

LOCALITY: Kaneohe Bay, Oahu, Hawaii.

TYPE SPECIMEN: *Pseudopecoeloides tenuoides,* deposited as no. 5613, Hancock Parasitology Collection.

Pseudopecoeloides tenuoides is closest to *P. tenuis,* described by Yamaguti (1940) from the small intestine of *Pseudopriacanthus nipponicus* (Cuv. et Valenc.), collected at Hamazima, Mie Prefecture, Japan. *P. tenuoides* differs from *P. tenuis* in having smaller eggs, a smaller oral sucker, smaller acetabulum, and in having acetabular pads.

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TID-5748

HEALTH AND SAFETY

A STUDY OF THE POSSIBLE RELATIONSHIP BETWEEN RADIOACTIVITY AND TOXICITY IN FISHES FROM THE CENTRAL PACIFIC

By
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May 1960
[TIS Issuance Date]

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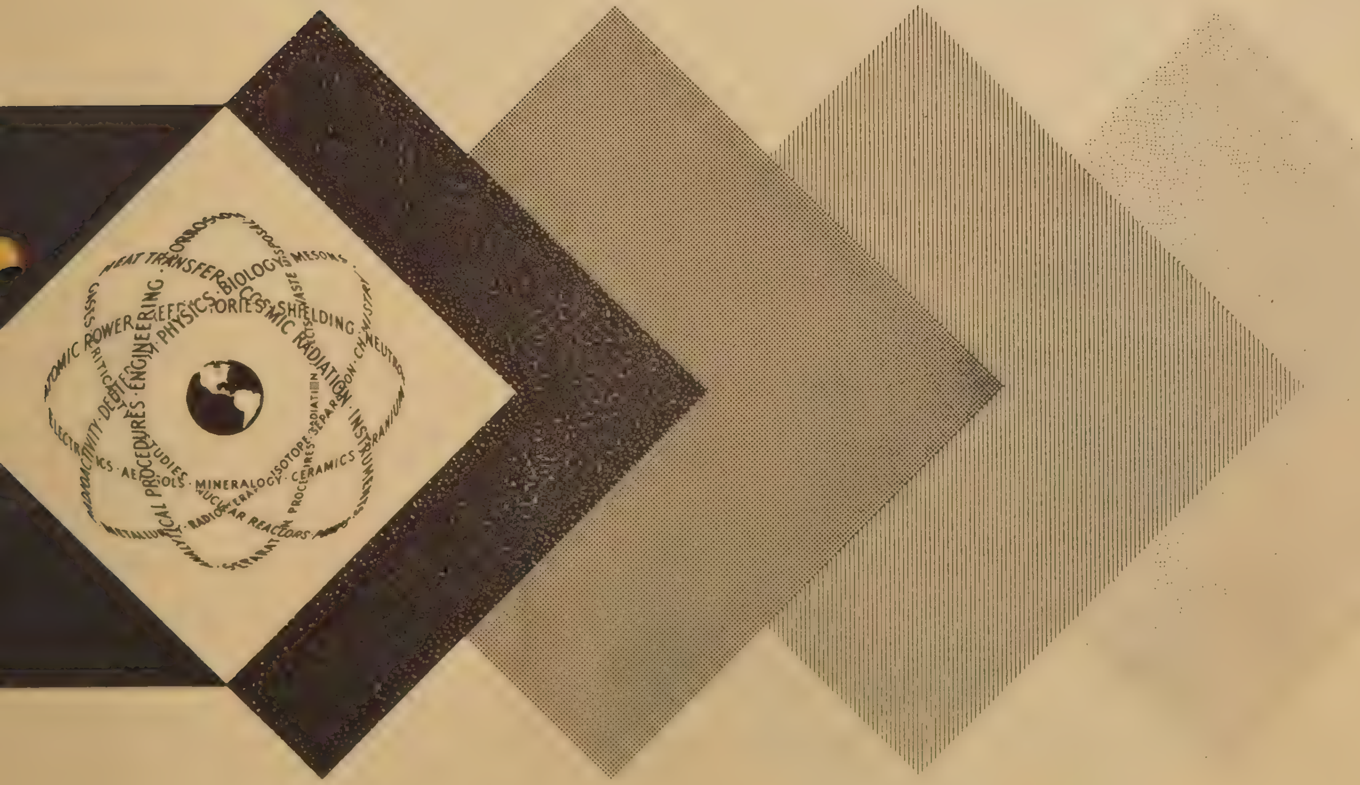
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Work performed under Contract No. AT(04-3)-235.

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A STUDY OF THE POSSIBLE RELATIONSHIP BETWEEN RADIOACTIVITY AND TOXICITY IN FISHES FROM THE CENTRAL PACIFIC

by

Philip Helfrich

Assistant Marine Biologist

Introduction

Fishes that are poisonous to eat have, for many years, caused sickness and death among residents of a number of island groups throughout the central and south Pacific. Little is known about the condition, but on the basis of symptoms produced and the species involved, at least two major categories of fish poisoning are generally recognized. (1) Tetraodon poisoning, involving the puffers or balloon fish and porcupine fish, and (2) *Ciguatera*-type fish poisoning which may result from eating a wide variety of reef fishes such as the snappers (Lutjanidae), groupers (Serranidae), jacks (Carangidae), moray eels (Muraenidae), surgeonfishes (Acanthuridae), and others. *Ciguatera*-type fish poisoning is not the result of bacterial contamination but is probably due to toxic substances ingested by the fish.

In recent years *Ciguatera*-type fish poisoning has been reported from island groups never before affected; and areas where the condition had been known for many years experienced a marked increase in the number of persons stricken. For example, the Line Islands in the central Pacific (about 1,000 miles south of Hawaii) were free of toxic fish until just prior to World War II. At the present time these islands (with the exception of Washington Island) appear to harbor more toxic reef fish than any other area in the Pacific, although no comprehensive survey has been made. In the Marshall Islands, where this type of fish poisoning has been known for many years, the condition has suddenly worsened; the number of episodes of fish poisoning recorded by health officials between 1955 and 1957 increased several-fold (Bartsch, Drachman, and McFarren, 1959). Marshallese natives have attributed the sudden increase in Ciguatera-type fish poisoning to the nuclear testing program. In order to determine if any relationship exists between radioactivity and toxicity of fishes, a continuing study has been undertaken by the Hawaii Marine Laboratory supported by the Atomic Energy Commission (Contract AT(04-3)-235 in conjunction with other studies on toxic marine organisms. This study was designed to determine if any correlation exists between radioactivity and Ciguatera-type toxicity in fishes. Fishes were screened for toxicity and radioactivity to check on possible etiological relationships, and the results are reported in this paper.

A more direct approach to the problem was also pursued, aimed at determining what factors in the environment could cause these fish to become toxic. The objectives are to discover the biological origin of the toxin, and to determine how the various organisms in a given environment obtain, metabolize, and transfer the toxin to other organisms. This includes an investigation of the ecology of the toxic species with emphasis on their food and feeding habits, as well as laboratory experiments on the transmission of the toxic element through the food chain and the distribution of the toxin in the affected fish. This ecological study will be reported on separately upon its completion.

In the initial phase of this survey, fishes from known "toxic" areas in the Marshall Islands were obtained and screened for toxicity and radioactivity. A majority of these fish were of the family Lutjanidae (snappers) which are well known for their poisonous qualities wherever toxic fishes are found, and samples were obtained from the Eniwetok and Majuro atolls. Of the fish studied, the flesh, liver, and gonads, the principal parts commonly used by the natives as food, were assayed for radioactivity; because of the small size of the visceral organs, only the flesh was assayed for toxicity. After a large number of fish from these two atolls were screened to determine if they were toxic, it was evident that the Marshall Islands could supply the investigation with few highly toxic fish; most of those sampled were marginally "toxic" to "non-toxic" by present tests.

In the spring and summer of 1959, opportunities were afforded the author to collect fishes at Palmyra and Christmas Island in the Line Islands, and a number of specimens of Lutjanus bohar (a large red snapper) were obtained for the investigation. Because both of these islands had reported cases of fish poisoning, and because Christmas Island has been the recent site of nuclear tests by the British government, it was felt that samples from this area would allow a contrast between radioactivity and toxicity in these fishes to be made as a supplement to data obtained in the Marshall Islands.

Procedures

Fish screened in this study were all taken on hook and line and placed in a freezer within four hours of capture. These frozen specimens were then returned to the laboratory, where tissues to be analyzed were removed and a portion weighing from 10 to 50 grams (depending on the size of the specimen) was placed in a crucible and ashed at 500° Centigrade for 12 hours. The ash was then weighed, and the ash weight as a percentage of wet weight thereby calculated. The ash from each sample was pulverized and triplicate samples weighing 4-8 mg. were prepared. These were mixed with a drop of distilled water to form a slurry which was spread on the planchettes to cover an area of approximately 3 $cm.^2$. The planchettes were then dried under infrared heat lamps, weighed, and analyzed for beta activity. The initial beta analysis was carried out using a Nuclear-Chicago Model 161-A scaler equipped with a D-34 G-M tube (window density of 1.4 $mg./cm.^2$) operated at 900 volts, preset for 1280 counts. After 1 July 1959, beta activity was measured with a Nuclear-

Chicago Model D-47 gas flow chamber using "Q-Gas" (98.7% helium, 1.3% butane) at 5 p.s.i., with a "Micromil" window (density less than 150 micrograms/cm.^{2}) at 1250 volts, preset for 1000 counts. Background blanks were counted twice daily when the D-34 tube was in use and between every two samples in the later analyses; samples were corrected for background by the application of an average of the two proximate control readings. The counting time required to obtain reasonable accuracy for low counts (of the order of those found in most of the samples analyzed) was calculated from the formulae and tables of Aronoff (1956; 56-62 and appendixes) and Kinsman (1957; 128-136). The beta counting error did not exceed 4%, and in most of the samples counted, the error was between 2 and 2½%. In order to determine the radioactivity of specimens at the time of capture, samples were recounted for beta activity approximately 180 days after the initial analysis. Of the samples of tissue that had not decayed to within the range of variation of background, the average rates of decay were plotted and the half lives and activities at the time of capture were calculated graphically. This calculation was based on the assumption that the decay curve of the sample did not differ significantly from an exponential curve.

The remaining ashed tissue from each fish was placed in a glass vial and analyzed for gamma activity in a Nuclear-Chicago Model DS 5-5 Scintillation Well Counter (NaI crystal treated with Thallium) with a Nuclear-Chicago Model 1810 Radiation Analyzer. This was operated with an open base (recording the full energy spectra of emitters) at 2500 volts, preset for 1280 counts. The gamma counting error did not exceed 10%, and in a majority of counts, the error was between 3% and 7%.

The toxicity of the fish sampled was determined by feeding the flesh to test animals and recording the maximum response in the first 48 hours after ingestion. The common mongoose Herpestes mungo was found to be sensitive to the toxin, and a rough scale of responses to various doses of the toxin was observed. The classification used to determine the relative toxicity of fish screened is presented in Table I.

TABLE I

CLASSIFICATION OF TOXIC FISH ACCORDING TO RESPONSE IN MONGOOSES

Scale of response[1]	Observable symptoms[2]	Classification	Symbol
0	None	NON-TOXIC	-
1	Slight weakness; flexion of fore limbs	MILDLY TOXIC	X
2	Slight motor ataxia, weakness in fore and hind limbs	MODERATELY TOXIC	XX
3	Moderate motor ataxia with weakness and/or partial paralysis of limbs and body musculature		
4	From acute motor ataxia and extreme weakness and/or paralysis (capable of only limited movement) to comatose	HIGHLY TOXIC	XXX
5 (death)	No respiratory movements		

---

[1] Greatest response observed to a dose equivalent to 10% of the body weight of the mongoose fed.

[2] In the first 48 hours after ingestion.

Different mongooses varied in their response to the same sample in doses of the same per cent body weight equivalent. Usually this variation in the response was greater in the more toxic categories, therefore the five categories of positive reactions that were recorded in the laboratory and listed in Table I are reclassified into three main groups for this study.

TABLE II

GROSS BETA AND GAMMA RADIOACTIVITY IN MUSCLE LIVER AND GONALS OF LUTJANID FISHES FROM THE MARSHALL AND LINE ISLANDS

DATE COLLECTED	LOCALITY	SPECIES	SAMPLE NO.	BETA ACTIVITY			GAMMA ACTIVITY			TOXICITY[3]
				AVER. MUSC.	CPM/MG. ASH[1] LIVER	GONADS	AVER. MUSC.	CPM/MG. ASH[2] LIVER	GONADS	
9/15/58	Eniwetok	*Lutjanus gibbus*	9-A-1	0.28	7.45					-
9/12/58	Majuro	*Lutjanus gibbus*	9-A-5	0.91						-
9/12/58	Majuro	*Lutjanus bohar*	9-B-4	0.08			0.03			-
9/12/58	Majuro	*Lethrinus miniatus*	9-H-1	0.11	6.76		0.84	18.76		XXX
9/12/58	Majuro	*Lethrinus miniatus*	9-H-2	0.19			0.53			X
10/3/58	Fanning	*Lutjanus bohar*	10-A-1	0.13			0.04			X
10/3/58	Fanning	*Lutjanus bohar*	10-A-2	0.18			0.03			X
10/3/58	Fanning	*Lutjanus bohar*	10-A-3	0.28			0.03			X
12/30/58	Eniwetok	*Lutjanus bohar*	12-B-1	0.11	5.30		0.65	46.14	1.93	-
12/30/58	Eniwetok	*Lethrinus miniatus*	12-C-1	BKGR.			0.04			-
12/30/58	Eniwetok	*Lethrinus miniatus*	12-C-2	0.63			0.51			-
12/30/58	Eniwetok	*Lethrinus miniatus*	12-C-5	0.54			1.03			-
12/30/58	Eniwetok	*Lutjanus gibbus*	12-D-2	0.33			0.72			-
1/8/59	Majuro	*Lutjanus bohar*	13-A-1	0.66			BKGR			XXX

TABLE II (continued)

DATE COLLECTED	LOCALITY	SPECIES	SAMPLE NO.	BETA ACTIVITY			GAMMA ACTIVITY			TOXICITY^3
				AVER. CPM/MG. ASH^1			AVER. CPM/MG. ASH^2			
				MUSC.	LIVER	GONADS	MUSC.	LIVER	GONADS	
1/8/59	Majuro	*Lutjanus bohar*	13-A-2	0.10	1.91		0.10			X
1/8/59	Majuro	*Lutjanus bohar*	13-A-3	0.09	0.47	0.21	0.02	0.10	0.21	XX
1/8/59	Majuro	*Lutjanus bohar*	13-A-4	0.05	0.18	0.56	0.28	0.05	0.10	X
1/8/59	Majuro	*Lutjanus bohar*	13-A-5	0.07	0.38	0.43	0.01	0.09	0.27	-
1/8/59	Majuro	*Lutjanus bohar*	13-A-6	0.02			0.02			-
1/8/59	Majuro	*Lutjanus bohar*	13-A-7	0.21	0.28	0.20	0.02	0.05	0.09	-
1/8/59	Majuro	*Lutjanus bohar*	13-A-11	0.41	2.69	0.46	0.02	0.49	0.55	-
1/9/59	Majuro	*Lutjanus bohar*	13-B-1	0.11	0.19	0.04	0.01	0.20	0.15	XX
1/9/59	Majuro	*Lutjanus bohar*	13-B-2	0.21			0.05			XX
1/9/59	Majuro	*Lutjanus bohar*	13-B-8	0.39	0.65	0.45	0.14	0.54	0.19	X
1/9/59	Majuro	*Lutjanus bohar*	13-B-12	BKGR	0.80	0.82	0.05	0.12	0.62	XX
1/9/59	Majuro	*Lutjanus bohar*	13-B-26		0.30	0.81		0.06	2.17	XX
1/9/59	Majuro	*Lethrinus miniatus*	13-C-1	0.72			0.19			-
1/8/59	Majuro	*Lutjanus gibbus*	13-D-3	0.86			0.07			-
1/8/59	Majuro	*Lutjanus gibbus*	13-D-4	0.27	2.41	0.30	0.03	0.16	0.08	-
1/8/59	Majuro	*Lutjanus gibbus*	13-D-7	0.33			0.37			-

TABLE II (continued)

DATE COLLECTED	LOCALITY	SPECIES	SAMPLE NO.	BETA ACTIVITY			GAMMA ACTIVITY			TOXICITY[3]
				AVER. MUSC.	CPM/MG. LIVER	ASH[1] GONADS	AVER. MUSC.	CPM/MG. LIVER	ASH[2] GONADS	
5/27/59	Palmyra	*Lutjanus bohar*	14-A-2	0.09	0.41	1.29	0.01	0.01	0.34	XXX
5/27/59	Palmyra	*Lutjanus bohar*	14-A-8	0.37	0.99	1.29	0.11	0.34	0.01	-
5/27/59	Palmyra	*Lutjanus bohar*	14-A-26	0.12	0.54		0.01	0.11		XXX
5/27/59	Palmyra	*Lutjanus bohar*	14-A-35	0.43	0.50		0.09	0.14	0.71	-
6/14/59	Christmas	*Lutjanus bohar*	16-A-2	0.06	0.10	0.05	0.01	0.06	0.03	XXX
6/14/59	Christmas	*Lutjanus bohar*	16-A-5	0.10	BKGR.	0.16	0.03	BKGR.	0.11	-
6/14/59	Christmas	*Lutjanus bohar*	16-A-12	0.11	0.06	0.02	0.01	0.04	0.03	XXX
6/14/59	Christmas	*Lutjanus bohar*	16-A-40	0.11	0.12	0.07	0.02	0.07	0.02	-

[1] Samples counted to 1280 counts except the 14 and 16 series which were counted to 1000 counts. Samples in the 9 through 13 series were counted 150 ± 20 days after collection, except for those reported in the preliminary report. Samples in the 14 series (Palmyra) were counted 46 ± 2 days after collection, and the 16 series (Christmas Island) 74 ± 3 days after collection.

[2] Samples counted to 1280 counts. Samples in the 9 through 13 series were counted 186 ± 13 days, except for those reported in the preliminary report. Samples in the 14 series (Palmyra) were counted 87 ± 6 days after collection, and the 16 series (Christmas Island) 80 ± 5 days after collection.

[3] Toxicity of muscle from mongoose feeding tests (as per Table I).
XXX strongly toxic
XX moderately toxic
X mildly toxic
- non-toxic

TABLE II (continued)

				BETA ACTIVITY			GAMMA ACTIVITY			
DATE COLLECTED	LOCALITY	SPECIES	SAMPLE NO.	AVER. MUSC.	CPM/MG. LIVER	ASH[1] GONADS	AVER. MUSC.	CPM/MG. LIVER	ASH[2] GONADS	TOXICITY[3]
1/8/59	Majuro	*Lutjanus bohar*	13-A-2	0.10	1.91		0.10			X
1/8/59	Majuro	*Lutjanus bohar*	13-A-3	0.09	0.47	0.21	0.02	0.10	0.21	XX
1/8/59	Majuro	*Lutjanus bohar*	13-A-4	0.05	0.18	0.56	0.28	0.05	0.10	X
1/8/59	Majuro	*Lutjanus bohar*	13-A-5	0.07	0.38	0.43	0.01	0.09	0.27	-
1/8/59	Majuro	*Lutjanus bohar*	13-A-6	0.02			0.02			-
1/8/59	Majuro	*Lutjanus bohar*	13-A-7	0.21	0.28	0.20	0.02	0.05	0.09	-
1/8/59	Majuro	*Lutjanus bohar*	13-A-11	0.41	2.69	0.46	0.02	0.49	0.55	-
1/9/59	Majuro	*Lutjanus bohar*	13-B-1	0.11	0.19	0.04	0.01	0.20	0.15	XX
1/9/59	Majuro	*Lutjanus bohar*	13-B-2	0.21			0.05			XX
1/9/59	Majuro	*Lutjanus bohar*	13-B-8	0.39	0.65	0.45	0.14	0.54	0.19	X
1/9/59	Majuro	*Lutjanus bohar*	13-B-12	BKGR	0.80	0.82	0.05	0.12	0.62	XX
1/9/59	Majuro	*Lutjanus bohar*	13-B-26		0.30	0.81		0.06	2.17	XX
1/9/59	Majuro	*Lethrinus miniatus*	13-C-1	0.72			0.19			-
1/8/59	Majuro	*Lutjanus gibbus*	13-D-3	0.86			0.07			-
1/8/59	Majuro	*Lutjanus gibbus*	13-D-4	0.27	2.41	0.30	0.03	0.16	0.08	-
1/8/59	Majuro	*Lutjanus gibbus*	13-D-7	0.33			0.37			-

TABLE II (continued)

DATE COLLECTED	LOCALITY	SPECIES	SAMPLE NO.	BETA ACTIVITY			GAMMA ACTIVITY			TOXICITY[3]
				AVER. MUSC.	CPM/MG. LIVER	ASH[1] GONADS	AVER. MUSC.	CPM/MG. LIVER	ASH[2] GONADS	
5/27/59	Palmyra	*Lutjanus bohar*	14-A-2	0.09	0.41	1.29	0.01	0.01	0.34	XXX
5/27/59	Palmyra	*Lutjanus bohar*	14-A-8	0.37	0.99	1.29	0.11	0.34	0.01	-
5/27/59	Palmyra	*Lutjanus bohar*	14-A-26	0.12	0.54		0.01	0.11		XXX
5/27/59	Palmyra	*Lutjanus bohar*	14-A-35	0.43	0.50		0.09	0.14	0.71	-
6/14/59	Christmas	*Lutjanus bohar*	16-A-2	0.06	0.10	0.05	0.01	0.06	0.03	XXX
6/14/59	Christmas	*Lutjanus bohar*	16-A-5	0.10	BKGR.	0.16	0.03	BKGR.	0.11	-
6/14/59	Christmas	*Lutjanus bohar*	16-A-12	0.11	0.06	0.02	0.01	0.04	0.03	XXX
6/14/59	Christmas	*Lutjanus bohar*	16-A-40	0.11	0.12	0.07	0.02	0.07	0.02	-

[1] Samples counted to 1280 counts except the 14 and 16 series which were counted to 1000 counts. Samples in the 9 through 13 series were counted 150 ± 20 days after collection, except for those reported in the preliminary report. Samples in the 14 series (Palmyra) were counted 46 ± 2 days after collection, and the 16 series (Christmas Island) 74 ± 3 days after collection.

[2] Samples counted to 1280 counts. Samples in the 9 through 13 series were counted 186 ± 13 days, except for those reported in the preliminary report. Samples in the 14 series (Palmyra) were counted 87 ± 6 days after collection, and the 16 series (Christmas Island) 80 ± 5 days after collection.

[3] Toxicity of muscle from mongoose feeding tests (as per Table I).
XXX strongly toxic
XX moderately toxic
X mildly toxic
- non-toxic

Discussion

The data presented in Table II do not show any marked relationship between levels of gross radioactivity and toxicity in the samples tested. Although some individual specimens show a low level of radioactivity with a high level of toxicity (for example, the highly toxic 16-A-2 displays a much lower level of beta activity than the non-toxic 9-A-1), a few other individual samples can be contrasted to show the opposite relationship. It is of interest to note that between tissues of the same specimen which were counted at approximately the same time, there appears to be a general tendency for the level of activity of the liver and gonads to exceed that of the muscle. These findings are in accord with other investigations of the radioactivity of various organs of reef fish from the Marshall Islands, indicating a probable greater accumulation of certain isotopes by the liver and gonads than by the muscle. Welander (1958; 5-12) found that in reef fish collected at Rongelap and Ailinginae Atolls from 1954 through 1958, the gross levels of beta and gamma radioactivity were consistently higher in the liver than in the muscle tissue; specific mention was not made of the gonads in his study. Thomas, Reid, and Lust (1958) also found that the gross beta activity was almost always higher in the liver than muscle tissue in fishes sampled from the Marianas and Caroline Islands in 1956. The significance of the higher levels of radioactivity in the liver and gonads analyzed in the present investigation is unknown. The significance of this observation requires a knowledge of the isotopes involved and further information on the biological mechanisms in fish for handling such isotopes.

Because the relationship of radioactivity to toxicity in fish is of interest from the standpoint of possible effects on humans upon consumption, it seemed logical to contrast the two at the time of the fish's capture (at which time it might have been eaten by local inhabitants). Long-range tests indicate that there is no significant decrease in the toxicity of fish muscle tissue stored in a frozen state for a period of up to two years. Therefore, the toxicity of specimens determined up to 120 days after capture was assumed to be the same as the toxicity at the time of capture.

The relationship between the calculated beta activity at the time of capture and the toxicity of thirty-five samples of various tissues from both the Line and Marshall Islands specimens is presented in Figure 1. The activity of the beta emitters is expressed in cpm/mg. ash; the ash weight is a fairly constant percentage of the wet weight in these samples (muscle, 1.41% ± 0.51; liver, 1.49% ± 0.33; gonads, 1.46 ± 0.63), and therefore these figures are relatively comparable to the activity per unit of wet weight. The mean calculated radioactive half life of all samples was 222 days, however, considerable variation was encountered between samples (standard deviation = 158.5); no consistency was noted in the rate of decay of samples with regard to the tissue involved, the species of fish, or the geographical area from which the fish was obtained.

In order to contrast toxicity with radioactivity in the samples analyzed, it was necessary to assign quantitative values to degrees of toxicity (based on the classification in Table I) with a gradient from non-toxic to highly toxic divided into four categories equally spaced on the abscissa of Figure 1. The assumption that the units of toxicity from non-toxic to highly toxic can be expressed as equal categories is perhaps not completely valid, however, it permits an examination of the data for possible trends. Expressed in this manner in Figure 1, these data reveal a general trend toward a negative regression of radioactivity on toxicity. This trend is more pronounced among the samples of muscle tissue than among the liver and gonad samples analyzed. A trend line of all samples (fitted by the method of least squares) indicates a slight negative slope. These data tend to confirm the

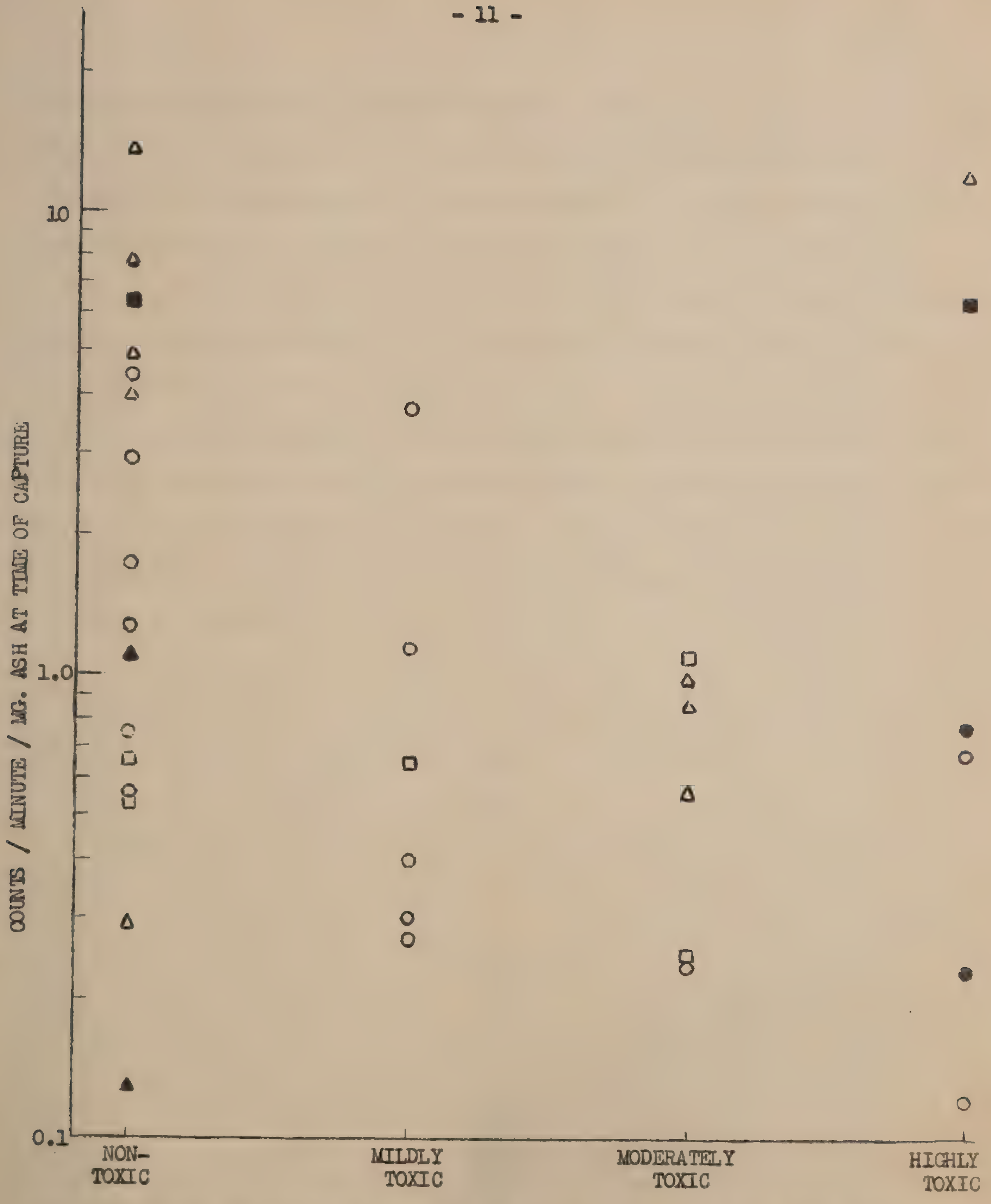

Figure 1. Gross beta activity at time of capture of tissues from fish of varying toxicities from the Marshall and Line Islands.
Symbols: ○ = muscle; △ = liver; □ = gonads. Open symbols represent Marshall Island specimens; solid symbols represent Line Island specimens.

hypothesis that there is no marked relationship between radioactivity and toxicity in these samples. The difficulties that arise in the numerical expression of toxicity do not permit a more sophisticated statistical analysis of these data.

The gross gamma radioactivity data presented in Table II were not corrected to capture time because a large number of the samples were within the range of background variation upon recounting. Estimation of the half-life of the most active samples indicated that they have a half-life of about two years. If this can be used as an indication of the rate of decay of all samples analyzed for gross gamma activity, the data presented in Table II may be considered close to that which existed at the time of capture. From the activity of individual samples, it can be concluded that there is no correlation between gross gamma activity and toxicity; these data as a group also show a trend toward decreased activity with increased toxicity.

Although facilities were available for gamma spectra analysis and chemical separation of isotopes, these were not attempted because such procedures would have been extremely time-consuming with the present staff and equipment; such an expenditure of time was not considered practical in light of the amount of information to be gained. Emphasis was placed on recording only the gross activity of samples of those portions of a fish most likely to be eaten. Previous reports on the radioactivity of fishes, however, suggest certain isotopes that might be constituents of these samples. Lowman, Palumbo, and South (1957) attributed 35-58% of the total activity of fish livers to Zn^{65} in a survey of marine animals in the Northern Marshall Islands. Thomas, Reid, and Lust (1958) concluded that Zn^{65} was the major radioisotope in fish as the result of an analysis of specimens (including a number of "snappers") from the Marianas and Caroline Islands. Welander (1958) found that Zn^{65} was a prominent, and often the dominant isotope in the liver and muscle of fishes from Rongelap and Ailinginae Atolls in the Marshall Islands. He notes that Zn^{65} "has consistently been found in fish tissue, usually as the dominant radioisotope." This is in agreement with the findings of at least ten other similar surveys. Welander also found Co^{57}, Co^{58}, and Co^{60}, as well as Fe^{55}, using both gamma spectrometry and chemical separation techniques. Using gamma spectrometry, Bartsch, Drachman, and McFarren (1959) found that Zn^{65} was the only obvious radioisotope of any consequence that appeared in samples of fish from Majuro Atoll in the Southern Marshall Islands. Based on these findings, Zn^{65} appears to be the most likely cause of the high activity recorded in some of the samples of liver in the present survey. The half lives of many of the samples analyzed for beta emissions in this survey were close to that for Zn^{65} (250 days), and Co^{57} (270 days).

Other Considerations

A lack of any correlation between toxicity and radioactivity in reef fishes of the Central Pacific as indicated by this investigation is not unexpected when the following pertinent points are considered:

1. The history of Ciguatera-type fish poisoning antedates nuclear contamination in the Pacific and elsewhere. Older residents of Jaluit Atoll in the Southern Marshall Islands speak of poisonous fish as a condition that has persisted for generations. Steinbach (1895), a medical officer in the Marshall Islands in 1893-94, reported that many species of fish were considered poisonous and indicated that he frequently encountered cases of fish poisoning among the local residents. The condition described leaves little doubt that it is the same type of fish poisoning (Ciguatera) encountered today. Numerous Japanese scientists investigated this poison fish problem in the Marshall Islands between 1923 and 1943 (Hiyama, 1943) indicating that it persisted as a serious problem in that area for at least a half

century before the first nuclear detonation. The condition is more recent in the Line Islands, where fish poisoning was unknown before 1935, however, it became a serious problem to the inhabitants of all of these islands (except Washington Island) by 1942 (Palmer in Randall, 1958; Ross, 1947). In addition, numerous cases of fish poisoning have been reported from other areas in the Pacific and Caribbean during the past hundred years.

2. The general syndromes of fish poisoning and ratiation sickness are distinct; early neurological involvement characteristically present in Ciguatera-type fish poisoning is absent in even acute cases of radiation sickness. Characteristic symptoms of radiation sickness such as changes in the abundance of formed elements in the blood has not been observed in victims of Ciguatera-type fish poisoning. The levels of radioactivity experienced in samples analyzed in this survey are not of sufficient magnitude to produce any symptoms of radiation sickness upon the ingestion of these fish in normal quantities.

3. Some species of pelagic fish taken from the proximity of nuclear test areas (tunas and wahoo (Acanthocybium solandri)) have been reported to have a high level of radioactivity, but these same species have never been implicated in a case of Ciguatera-type fish poisoning.

Conclusions

1. The accumulated data show an absence of any correlation between radioactivity (gross beta and gamma activity) and Ciguatera-type toxicity in samples of muscle, liver, and gonads from lutjanid fishes from the Marshall and Line Islands.

2. In a high per cent of the samples tested, the liver was more radioactive than the gonads and muscle. Only rarely was the muscle more active than the gonads and/or liver.

3. The mean half life of thirty-five beta activity samples was calculated to be 222 days. No consistency was observed in the rate of decay of samples in regard to the tissue involved, the species of fish, or the geographical area from which the fish was obtained.

4. Comparison of the results of previous surveys and the beta half life of samples analyzed in this investigation suggest Zn^{65} and possibly Co^{57} are probable constituents of the samples analyzed.

5. Absence of any correlation between Ciguatera-type toxicity and radioactivity in fishes of the Central Pacific is reasonable in the light of (a) the history of fish poisoning which antedates all nuclear detonations, (b) the distinct syndromes in radiation sickness and fish poisoning, and (c) the complete absence of toxicity in groups of fishes known to have been radioactive.

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